THESIS

WOLF PACK DYNAMICS AND MOVEMENTS IN RESPONSE TO HARVEST ON THE KENAI NATIONAL WILDLIFE REFUGE, ALASKA, 1982-1993

AND

ACCURACY OF AERIAL TELEMETRY

Submitted by

Elizabeth Anna Jozwiak

Department of Fishery and Wildlife Biology

In partial fulfillment of the requirements

for the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 1997

COLORADO STATE UNIVERSITY

October 27, 1997

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY ELIZABETH ANNA JOZWIAK ENTITLED WOLF PACK DYNAMICS AND MOVEMENTS IN RESPONSE TO HARVEST ON THE KENAI NATIONAL WILDLIFE REFUGE, ALASKA, 1982-1993, AND ACCURACY OF AERIAL TELEMETRY LOCATIONS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

Rodney Y. Bailey

Philip N. Omi

Gary C. White

William F. Andelt

Advisor

Mark P. Conner

Department Head

ABSTRACT OF THESIS

WOLF PACK DYNAMICS AND MOVEMENTS IN RESPONSE TO HARVEST ON THE KENAI NATIONAL WILDLIFE REFUGE, ALASKA, 1982-1993

AND

ACCURACY OF AERIAL TELEMETRY

One hundred and seven wolves (*Canis lupus*) were captured, radio-collared, and located 1,775 times from aircraft to determine the relationship between harvest and wolf pack size, territory size, density, and dispersal on the Kenai National Wildlife Refuge. Annual harvest averaged 61% from 1982/83 through 1985/86, and declined to 14% from 1986/87 through 1992/93. Territory sizes were not correlated with pack sizes (r = 0.22, 48 df, P = 0.132) or annual harvest rates (r = -0.23, 48 df, P = 0.110). Wolf dispersal from packs increased when harvest was low (χ^2 = 11.73, 1 df, P = 0.001), with a greater proportion per year of juveniles dispersing (χ^2 = 8.07, 2 df, P = 0.018) than adults or pups. Early winter wolf density averaged 13.4 wolves/1,000 km^2, and ranged from 17.0 in 1983/84 to 9.4 in 1985/86. Pack sizes and annual wolf densities were not correlated (r = 0.09, 50 df, P = 0.520; r = 0.06, 10 df, P = 0.864, respectively) with level of harvest, thus other factors such as low pup recruitment and a declining moose population may have limited population growth during periods of reduced harvest.

I compared the accuracy of aerial telemetry locations obtained with a Global Positioning Satellite (GPS) unit and the same locations independently hand-plotted on a map by locating 12 radiocollars (6 visible from aircraft) in 3 habitats on 6 occasions on the Kenai National Wildlife Refuge during 1993-1994. Accuracy of the GPS ($\bar{x}$ = 139.1 m, SE = 9.65) and map-plotted ($\bar{x}$ = 168.4 m, SE = 21.9) locations was not found different (F = 2.39; 1, 36 df; P = 0.131). Accuracy was not found to differ by habitat type (F = 1.01; 2, 36 df; P = 0.373), or by visibility of the collar (F = 2.91; 1, 36 df; P = 0.097). Accuracy of the GPS method improved with successive trials (contrast F = 20.57; 1, 5 df; P = 0.0001). I examined aircraft heading and GPS error ($\bar{x}$ = 81.4 m, SE = 7.63) by locating 5 ground reference points 1-4 times each for a total of 17 locations from the air, and determined that the pilot activated the GPS unit 1-2 seconds before passing over the point which contributed to error. Test flights should be conducted before data collection to determine the optimal time to activate the GPS unit to minimize error. I recommend the GPS system over map plotting of aerial telemetry locations because of ease of use, and ability to download data directly to a computer for analysis.

Elizabeth Anna Jozwiak
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523
Fall 1997

DEDICATION

I dedicate this thesis to the memory of my father, Klemens F. Jozwiak. He taught me to respect and value wildlife and to enjoy the beauty of wild places. His love of nature was a great influence in my life, and I will always be grateful.

ACKNOWLEDGMENTS

This study would not have been possible without the assistance and support of numerous agencies and individuals during the past 10 years. The staff and volunteers at the Kenai National Wildlife Refuge captured wolves and assisted with collecting radiotelemetry data. The Alaska Department of Fish and Game, namely, Ted H. Spraker and Dr. Chuck C. Schwartz, provided valuable assistance in the field. Vernon Lofstedt and Craig Lofstedt of Kenai Air piloted helicopters during wolf capture efforts. Richard E. Ernst served as the pilot during the aerial telemetry study. The Kenai National Wildlife Refuge and Rick Plate from the Alaska Division of Forestry, Soldotna, Alaska provided GPS equipment and logistical assistance. Youth Conservation Corp students assisted with operation of the Killey AZ base station. Special thanks to Scott McLane of McLane and Associates, Soldotna, Alaska and Ed Carlson of the National Geodetic Survey for contributing technical advice on data collection and GPS post-processing.

I am especially grateful to the Rob and Bessie Welder Wildlife Foundation for providing me with a 2 year fellowship. The College of Natural Resources, Colorado State University provided tuition assistance. The U.S. Fish and Wildlife Service (USFWS) provided logistic support.

I wish to thank my advisor, Dr. William F. Andelt, who assisted with study design, and provided valuable suggestions for improving the manuscript. My supervisor and adjunct committee member, Dr. Theodore N. Bailey supported my efforts in the field, and served as the observer during the aerial telemetry study. Their guidance throughout this project was exceptional, and very much appreciated. Many thanks to my committee members Dr. Philip N. Lehner and Dr. Gary C. White for reviewing the manuscipt, and for their advice and refreshing viewpoints on the graduate experience. Dr. William C. Gasaway and Ted H. Spraker reviewed an earlier draft of chapter 1. Dr. Kenneth P. Burnham, Dr. Phillip L. Chapman, and Dr. Gary C. White provided statistical assistance. A heartfelt thank you to my mother, my family, and to friends and coworkers at the Kenai National Wildlife Refuge for their support and encouragement during the thesis writing period. Some acknowledgment should also go to the 107 wolves studied on the Kenai Peninsula, because without them this research would not have been possible.

TABLE OF CONTENTS

CHAPTER 1

WOLF PACK DYNAMICS AND MOVEMENTS IN RESPONSE TO HARVEST ON THE KENAI NATIONAL WILDLIFE REFUGE, ALASKA, 1982-1993.

CHAPTER 2

ACCURACY OF AERIAL TELEMETRY.

Chapter 1

WOLF PACK DYNAMICS AND MOVEMENTS IN RESPONSE TO HARVEST ON THE KENAI NATIONAL WILDLIFE REFUGE, ALASKA, 1982-1993

Key words: *Canis lupus*, density, dispersal, home range, Kenai peninsula, management, population dynamics, radio telemetry, territoriality.

INTRODUCTION

Wolf management varies widely across North America. Wolves that naturally recolonized portions of northern Minnesota, Wisconsin, Michigan, and Montana are protected, but wolves reintroduced to central Idaho and Yellowstone National Park are managed as an experimental population (Fritts et al. 1994, Bangs and Fritts 1996). In Alaska, wolves are managed as a game animal, and in some areas their numbers are reduced to increase ungulate densities for human harvest (Stephenson 1978, Van Ballenberghe 1981, Theberge and Gauthier 1985, Boertje et al. 1996). The wolf is also important for its non-consumptive value to visitors of Alaska's national parks, refuges, and wilderness areas (Alaska Division of Tourism 1993). To effectively manage wolves under these multiple scenarios, wildlife managers need a comprehensive understanding of the factors that regulate wolf populations and the impacts of human caused mortality.

Wolves were numerous on the Kenai Peninsula before 1890, but were eliminated by humans by 1909 (Palmer 1938). The use of poison, unregulated hunting and trapping, and predator control programs during the 1940's and 1950's probably prevented wolves from becoming reestablished (Peterson and Woolington 1982). Hunting and trapping of wolves was closed in 1961 to allow them to recolonize. By the late 1960's, large packs were observed. Hunting and trapping for wolves was authorized in 1974, and has continued to present.

Peterson et al. (1984) reported human harvest to be the primary regulator of wolf density on the Kenai peninsula between 1976-1981. Annual harvests >40% reduced wolf densities, pack sizes, and size of pack territories. Wolf harvest on the Kenai peninsula declined after 1986 due to the combined effects of severe winter weather, new trapping regulations, pelt damage caused by the biting dog louse (*Trichodectes canis*) (Schwartz et al. 1983), and declining fur values. Keith (1983) suggested that wolf populations declined when harvests exceeded 38% of fall densities. Wolf populations also declined when the combined effects of harvest and wolf control removed 38-61% of the early winter wolf population in interior Alaska (Gasaway et al. 1983, 1992, Boertje et al. 1996), and >40% of the autumn population in Southcentral Alaska (Ballard et al. 1987). Potvin et al. (1992) reported wolf densities returned to their former level after a 40-71% reduction, primarily through immigration by the subsequent winter in Quebec.

Low availability of prey, habitat saturation, low social status, and intra-pack strife have been reported to encourage wolf dispersal (Fritts and Mech 1981, Van Ballenberge 1983, Peterson et al. 1984, Messier 1985a, Mech 1987, Fuller 1989, Gese and Mech 1991) however, few studies examined harvested populations. Ballard et al. (1987) hypothesized that dispersers were important in potentially minimizing inbreeding in exploited populations because exploited packs had a less rigid social system, and were more likely to accept dispersers.

I conducted this study because few longterm investigations have addressed the impacts of annual harvest on wolves. My objectives were to determine the relationships between wolf harvest and wolf densities, rates of dispersal, and territory sizes on the northwestern Kenai peninsula between 1982-1993. I also determined if dispersal rates of wolves were correlated with wolf densities and pack sizes.

STUDY AREA

The Kenai Peninsula (26,000 km^2) is located in southcentral Alaska approximately 40 km south of Anchorage (Lat. 60° N, Long. 150° W). It is connected to mainland Alaska by a 16 km wide section of land and ice. The study area is located in the northern portion of the Kenai National Wildlife Refuge (KNWR), and primarily encompasses 3,416 km^2 of Kenai lowlands in Game Management Subunit (GMS) 15A (Fig. 1).

Forested areas comprise approximately 50% of the study area, and are in various successional stages due to wildfires in 1947 and 1969. Moose (*Alces alces*) densities remained relatively stable in the residential and developed areas (585 km^2) (KNWR, unpublished data) and in the 1969 burn (475 km^2) from 1982 to 1990 because of the availability of early seral vegetation, but have declined in mature forest (1,106 km^2) and 1947 burn (1,250 km^2) habitats (Loranger et al. 1991).

Forest vegetation includes white spruce (*Picea glauca*), black spruce (*Picea mariana*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and willow (*Salix* spp). A detailed description of the vegetation is provided by Schwartz and Franzmann (1991).

METHODS

Wolves were captured in spring and summer with Newhouse 4, 14, and 114 double longspring, or offset-jawed Alpine 7 leghold traps. Traps were checked each morning. Trapped wolves were immobilized with phencyclidine hydrochloride (Sernylan, Parke-Davis Company, Saint Joseph, Missouri), ketamine hydrochloride (Ketaset, Fort Dodge Laboratories, Fort Dodge, Iowa), or tiletamine hydrochloride and zolazepam hydrochloride (Telezol, A.H. Robins Company, Richmond, Virginia). Wolves also were captured by darting from a helicopter in winter or early spring. Captured wolves were weighed, measured, ear-tagged, and fitted with 164-166 MHz radiocollars (Telonics, Mesa, Arizona).

Wolves were classified as pups (<1 year old), juveniles (1-2 years old), or adults (≥2 years old), based upon tooth eruption and wear, weight, and body size.

We attempted to capture and collar at least 1 wolf annually from all packs residing in the study area. Each collared wolf was located 1-4 times each month from a fixed-wing aircraft (PA-18 Supercub or Cessna 206) with strut mounted antennae (Gilmer et al. 1981). Locations from 1 December 1982 to 10 June 1992 were plotted on 1:63,360 topographic maps, and converted to Universal Transverse Mercator System (UTM) coordinates in the North American Datum (NAD) 27. An aircraft Global Positioning Satellite receiver (Trimble, Sunnyvale, California) was used to record locations of collared wolves from 10 June 1992 to 30 June 1993 which were converted to the NAD 27 projection using ARC/INFO Software (ESRI, Redlands, California). Telemetry locations <24 hours apart were eliminated from the analyses to reduce the effect of autocorrelation (Swihart and Slade 1985). The accuracy of GPS-collected and map-plotted telemetry locations were similar (see chapter 2).

Wolf pack territory size was estimated from 1 October through 30 April with the minimum convex polygon method (Mohr 1947) using program MCPAAL (Stüwe and Blohowiak 1985). This estimator was used to remain consistent with pack territory size calculations used by Peterson et al. (1984). All locations of pack members were combined to calculate territory size except when ≥2 radioed wolves from the same pack were located together, then one location was recorded. Winter pack locations were plotted using Simple Geographic

Language (SGL) software (Greslin 1992). Obvious movements outside the pack's territory, dispersal locations, and movements of lone wolves and pairs were excluded from the winter territory size estimation. Territory sizes are considered minimum use areas.

Areas estimated with the minimum convex polygon usually increase with added locations (Jennrich and Turner 1969). Ballard et al. (1987) defined wolf pack territories only when the size of areas for packs were not correlated with the number of days monitored (>60 pack locations). Pack territories were included in analyses with harvest and pack parameter variables because territories were not strongly correlated with the number of radiolocations ($r = 0.18$, 48 df, $P = 0.209$).

The maximum number of wolves observed in each pack from 1 December through 30 March was considered the minimum winter pack size. Wolves harvested prior to the date of the highest visual count(s) and within wolf territories, as determined from sealing records provided by the Alaska Department of Fish and Game, were added to the observed pack sizes. A pack was considered ≥ 3 wolves. If non-radioed packs were also present in the census area, pack sizes were determined by following fresh wolf tracks in snow from an aircraft until the pack was located visually. Minimum numbers of wolves present during winter were calculated by summing the maximum observed number of wolves in all radioed and non-radioed packs, adding wolves harvested prior to the highest pack count(s), and adding 15% (Wolf

Management Operational Plan, 1988, U.S. Fish and Wildlife Service, Soldotna, Alaska) to the estimate for lone wolves and pairs in the population. Density was determined by dividing the wolf population estimate by the GMS 15A census area (3,416 km^2).

Collared wolves were considered to disperse if they moved >1/2 the diameter of their pack's territory outside the territory boundary, and did not return within a 12 month period. Forays were distinguished from dispersals if individuals returned to their original pack territory within 12 months. If radio-contact was lost <2 weeks after a wolf had made 1 or more movements outside its pack territory and was not observed visually, the wolf was assumed to have dispersed beyond the study area. Wolves were also considered to have dispersed if their radio transmitter failed while still in the original territory, but were later reported killed >50 km outside the pack's territory to distinguish it from a foray. A dispersal date was assigned as halfway between the last known location within the territory and when the wolf was harvested, or radiocollar retrieved. Annual dispersal rates were determined from 1 September through 31 August. The proportion of collared wolves that dispersed each year was calculated by dividing the number of collared wolves that dispersed by the total number of wolves wearing functional collars during the monitoring period.

Wolves were harvested by hunters from 10 August to 30 April between 1982-1993, and harvested by trappers from 10 November to 31 March between 1982-1988, and from 10 November to 28 February between 1989-1993.

Because wolves must be sealed by the Alaska Department of Fish and Game within 10 days of harvest, the pelt sealing statistics provided seasonal totals of the number of wolves legally harvested in the study area.

The effect of age, sex, annual harvest, pack size, and pack affiliation on dispersal was determined with likelihood ratio tests (PROC GENMOD, SAS Institute, 1993). The most parsimonious model was chosen using Akaike's Information Criterion (AIC) (Akaike 1973, Burnham and Anderson 1992). Sex ratios and age structure of captured wolves were compared with likelihood-ratio Chi-squared statistics. Correlations (PROC CORR, SAS Institute, 1993) were used to determine the relationships between pack size and territory size, harvest and density, and yearly harvest and territory size and pack size.

RESULTS

Seventy-eight wolves (39 M, 39 F) initially were darted from a helicopter in winter, and 29 wolves (11 M, 18 F) initially were trapped in summer between 1982-1993 (Appendix 1). Of these, 73 (32 M, 42 F) were captured once, 26 (14 M, 12 F) were captured twice, 6 (3 M, 3 F) were captured 3 times, and 2 (1 M, 1 F) were captured 4 times. Annual relocations in winter averaged 8.1/wolf (range = 3-30), and 21.0/pack (range = 4-65) from 1 October 1982 through 30 April 1993. Sex ratios and the ratio of adults to juveniles and pups captured did not differ among years ($\chi^2 = 8.88$, 10 df, $P = 0.544$; $\chi^2 = 14.66$, 10 df, $P = 0.145$, respectively).

Radio contact was maintained with 4 to 6 packs each year. Average annual pack sizes ranged from 5.6 to 10.5 wolves, and individual packs ranged from 3 to 16 wolves (Table 1, Appendix 2). The minimum wolf population estimate in GMU 15A ranged from 32 to 58.

Average yearly pack territory sizes ranged from 239.0 to 851.4 km^2 (Fig. 2), and did not correlate with observed pack sizes (Table 2). The relationship of territory size to the previous year's pack size was significant only for the Bear Lake Pack (Table 2). Territory boundaries overlapped with other adjacent packs, did not remain consistent from year to year (Appendix 8), and boundary overlaps were most evident in years that harvest was low and dispersal was high (Appendix 9). Several pack members were located with members of other packs, or in other pack territories during extraterritorial movements before returning to their original packs. From 1982/83-1992/93, one of the largest pack territories (Point Possession) was located in the northern portion of the peninsula where mature forest is the major habitat and winter moose densities were low (1982-1990: <0.1-1.1 moose/km^2, KNWR, unpublished data). Concurrently, 2 adjacent packs with smaller territories resided either within the 1969 burn (Elephant Lake pack) or the 1947 burn (Bear Lake pack) habitat where moose densities were higher (1982-1990: 2.7-6.0 moose/km^2, 0.1-1.6 moose/km^2, respectively, KNWR, unpublished data). During the late 1970's, the Swanson River pack occupied most of the 1969 burn habitat (Peterson et al. 1984). After moose densities increased in the early 1980's (Loranger et al.

1991), the area was occupied by 3 packs including the Swanson River Pack which occupied only one third of its original range.

An average of 61% of the wolf population was harvested annually between 1982/83-1985/86, but harvest levels declined to an average of 14% from 1986/87 to 1992/93 (Table 1). Wolf density was similar during years of high harvest (1982/83-85/86; 13.5 wolves/1,000 km^2) and years of low harvest (1986/87-92/93; 13.4 wolves/1,000 km^2), and was not found related to harvest rates ($r = 0.06$, 10 df, $P = 0.864$). Territory size and pack size were not correlated with harvest ($r = -0.23$, 48 df, $P = 0.110$; $r = 0.09$, 50 df, $P = 0.520$, respectively) (Table 3). Pack size averaged 8.5 and 8.2 wolves in high and low harvest years, respectively.

Dispersal was not found related to sex, pack size, or pack affiliation, but was related to age and annual harvest (AIC = 134.9) (Fig. 3). A greater percentage of collared wolves dispersed when the annual wolf harvest was low (25.0%) than when harvest was high (9.3%) ($\chi^2 = 11.73$, 1 df, $P = 0.001$), and more juveniles (38%) than adults (23%) or pups (3%) dispersed each year ($\chi^2 = 8.07$, 2 df, $P = 0.018$). Five of 30 dispersing wolves (3 M, 2 F) joined adjacent packs, 11 (6 M, 5 F) joined a collared disperser from another pack and established territories on the Kenai peninsula, 2 (1 M, 1 F) were killed by other wolves, 4 (3 M 1 F) dispersed to the mainland, 4 (1 M, 3 F) were harvested, 1 (1 M) was killed illegally, and the status of 3 (3 M) was undetermined (Appendix 7). Wolves dispersed most frequently in January and February (6 each month), 4 dispersed in April, 2 each in March and June, and 1 each in May, November, and December. Wolves either made several temporary excursions from the pack territory, roamed its periphery, and reunited several times with pack members before eventually dispersing; or wolves moved from the original pack into a neighboring territory with no detected forays. Fifteen of 30 wolves (10 M, 5 F) dispersed from the GMS 15A study area.

DISCUSSION

A declining wolf harvest on the KNWR did not result in an overall increase in wolves. In contrast, Fritts and Mech (1981), Gasaway et al. (1983), and Ballard et al. (1987) reported that wolf density increased quickly when wolves were no longer hunted or controlled. The higher frequency of wolves dispersing from packs was associated with lower harvest but likely did not reduce density because only 4 of 30 (13%) dispersing wolves left the Kenai Peninsula during the entire study. Rates of dispersal from packs on the KNWR did not increase until 4 years after harvest declined, when 11 of 21 (52%) wolves left the GMS 15A study area between 1 September 1990 and 31 August 1993. While movement to and from the mainland is probably low, wolves from other areas of the Kenai peninsula may have immigrated to GMS 15A , therefore net dispersal could not be determined. In addition to high dispersal rates, shifts in pack territory boundaries and overlaps with other packs were evident during years of lower harvests. This behavior has been documented elsewhere in Alaska (Van Ballenberge 1983, Meier et al. 1995).

Declining moose densities in the 1947 burn habitat may have affected wolf population growth and dispersal. Messier (1985b), Ballard et al. (1987), and Peterson and Page (1988) documented higher rates of dispersal in areas of declining prey density. Prey vulnerability in recent years may also have declined. The age structure of Kenai moose has changed since the 1970's from primarily 12-18 year old moose (Peterson et al. 1984) to younger adults (KNWR, unpublished data) which are less vulnerable to wolves (Peterson et al. 1984).

I hypothesized that lower harvests would increase pack size and the size of territories. However, harvest levels were not found to affect pack size and territory size in this study. Peterson et al. (1984) reported that increased harvests resulted in smaller packs and territories, and in establishment of new packs in vacant areas. During 1976-1981, wolves were recent recolonizers, and were expanding into vacant territories when moose densities were high in the 1947 burn habitat, and the availability of food was not limiting wolf numbers (Peterson et al. 1984). The lack of increase in wolf pack size may have been related to a decline in moose density. It is also likely that I was unable to detect a relationship between pack size and territory size because fewer relocations were used to estimate territory size of wolf packs in this study (1,775 vs. 3,600 telemetry locations from Peterson et al. 1984), and territory size may have been underestimated.

Litter sizes and pup recruitment were not observed, and may have contributed to reduced pack size. Mech and Goyal (1995) reported that the prevalence of the canine parvovirus antibody was related to decreased wolf pup recruitment and winter wolf population declines when canine parvovirus antibody prevalence was found in >76% of wolves tested. Canine parvovirus is fatal to dog pups (Eugster and Nairn 1977) and captive wolf pups (Mech and Fritts 1987), and may also have caused wolf pup mortalities in Glacier National Park (Johnson et al. 1994). Bailey et al. (1995) reported that the canine parvovirus antibody occurred in 17% (n = 30) of Kenai wolves >12 weeks old during 1976-81 but increased to 64% during 1983-88 (n = 25). Pups also comprised a lower percentage of the wolves harvested during 1985/86-1992/93 (15.3%) than during 1981/82-1985/86 (45.3%) suggesting that fewer pups survived to 1 year of age during the later years of the study. The prevalence of the canine parvovirus antibody has been reported as contributing to recent declines in the Isle Royale wolf population (Peterson 1996) and to the slow increase of wolves in Wisconsin (Wydevan et al. 1995). Similarly, Ballard et al. (1997) reported that rabies may have been a significant factor limiting wolf growth in northwest Alaska, and suggested that dispersal increased from the effects of disease because the pack social structure was disrupted following mortalites.

While causal relationships cannot be inferred from observational data (Cook and Campbell 1979), the benefit of longterm data is to identify apparent trends and formulate research questions for further study. Wolves did not respond to a declining wolf harvest by increasing density as hypothesized. From indirect evidence, I suggest that wolf population growth during 1985/86 -1992/93 may have been limited by lower prey availability in the 1947 burn habitat, and reduced pup survival and recruitment. The effect of prey availability and exposure to the canine parvovirus antibody on wolf population dynamics should be explored on the KNWR in the future.

LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Alaska Division of Tourism. 1993. Alaska visitor statistics program, Summer 1993. Department of Commerce and Economic Development, Juneau, Alaska, USA.

Bailey, T. N., E. E. Bangs, and R. O. Peterson. 1995. Exposure of wolves to canine parvovirus and distemper on the Kenai National Wildlife Refuge, Kenai Peninsula, Alaska, 1976-1988. Pages 441-446 *in* L.N. Carbyn, S.H. Fritts, and D.R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occassional Publication 35, University of Alberta, Edmonton.

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135.

_____, J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in southcentral Alaska. Wildlife Monographs 98.

Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin 24:402-413.

Boertje, R. D., P. Valkenburg, and M. E. Mcnay. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60:474-489.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16-30 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: Populations. Elsevier Science. London, England.

Cook, T. D., and D. T. Campbell. 1979. Causal inference and the language of experimentation. Pages 1-9 *in* Quasi-Experimentation: Design and analysis issues for field settings. Houghton-Mifflin, Houghton, Michigan.

Eugster, A. K., and C. Nairn. 1977. Diarrhea in puppies: Parvovirus-like particles demonstrated in their feces. Southwest Veterinarian 30:59.

Evans, C. D., W. A. Troyer, and C. J. Lensink. 1966. Aerial census of moose using quadratic sampling units. Journal of Wildlife Management 30:767-776.

_____, E. E. Bangs, J. F. Gore. 1994. The relationship of wolf recovery to habitat conservation and biodiversity in the northwestern United States. Landscape and Urban Planning 28:23-32.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Sheperd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84.

_____, R. D. Boertje, D. . V. Grangaard, D. J. Reed, and S. J. Harbo. 1986. Estimating moose population parameters from aerial surveys. Biological Papers of the University of Alaska 22.

_____, _____, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120.

Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969-1989. Canadian Journal of Zoology 69:2946-2955.

Gilmer, D. S., L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaiffer, and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U. S. Fish and Wildlife Service Resource Publication 140.

Greslin, J. 1993. Simple Geographic Language (SGL), National Biological Survey, Fairbanks, Alaska, USA.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227-237.

Johnson, M. R., D. K. Boyd, and D. H. Pletscher. 1994. Serology of canine parvovirus and canine distemper in relation to wolf (*Canis lupus*) pup mortalities. Journal of Wildlife Diseases 30:270-273.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66-77 *in* L. N. Carbyn, editor. Wolves in Canada and Alaska: their status, biology, and management. Canadian Wildlife Service Report Series 45.

Loranger, A. J., T. N. Bailey, and W. W. Larned. 1991. Effects of forest succession after fire in moose wintering habitats on the Kenai Peninsula, Alaska. Alces 27:100-109.

Mech, L. D. 1987. Age, season, distance, direction, and social aspects of wolf dispersal from a Minnesota pack. Pages 55-74 *in* B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns: The effects of social structure on population genetics. University of Chicago, Chicago, Illinois, USA.

_____, and S. H. Fritts. 1987. Parvovirus and heartworm found in Minnesota wolves. Endangered Species Technical Bulletin 12, U.S. Fish and Wildlife Service, Washington D.C., USA

_____, and S. M. Goyal. 1995. Effects of canine parvovirus on gray wolves in Minnesota. Journal of Wildlife Management 59:565-570.

Meier, T. J., J. W. Burch, L. D. Mech, and L. G. Adams. 1995. Pack structure and genetic relatedness among wolf packs in a naturally-regulated population. Pages 441-446 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35, University of Alberta, Edmonton.

Messier, F. 1985a. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63:239-245.

Messier, F. 1985b. Social organization, spatial distribution, and population density of wolves in relation to moose density. Canadian Journal of Zoology 63:1068-1077.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Palmer L. J. 1938. Kenai Peninsula moose. Bureau of Biological Survey, U.S. Fish and Wildlife Service, Juneau, Alaska, USA.

Peterson, R.O. 1996. Ecological studies of wolves on Isle Royale. Annual Report 1995-1996. Isle Royale Natural History Association, Houghton, Michigan, USA.

_____, and R. E. Page. 1988. The rise and fall of Isle Royale wolves, 1975-1986. Journal of Mammalogy 69:89-99.

_____, and J. D. Woolington. 1982. The apparent extirpation and reappearance of wolves on the Kenai Peninsula, Alaska. Pages 334-344 *in* F. H. Harrington and P. C. Paquet, editors, Wolves of the world. Noyes, Park Ridge, New Jersey, USA

_____, _____, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88.

Potvin, F., H. Jolicoeur, L. Breton, and R. Lemieux. 1992. Evaluation of an experimental wolf reduction and its impact on deer in Papineau-Labelle Reserve, Quebec. Canadian Journal of Zoology 70:1595-1603.

SAS Institute, Inc. 1993. SAS/STAT User's Guide, Release 6.09 Edition, SAS Institute, Cary, North Carolina, USA.

Schwartz, C. C., R. Stephenson, and N. Wilson. 1983. *Trichodectes canis* on the gray wolf and coyote on the Kenai Peninsula, Alaska. Journal of Wildlife Diseases 19:373-375.

_____, and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113.

Stephenson, R. O. 1978. Unit 13 wolf studies. Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Annual Report W-17-8.

Stüwe, M., and C. E. Blohowiak. 1985. MCPAAL: Micro-computer programs for the analysis of animal locations. Conservation Research Center, Smithsonian Institute, Washington D.C., USA.

Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range. Journal of Wildlife Management 449:1019-1025.

Theberge, J. B., and D. A. Gauthier. 1985. Models for wolf-ungulate relationships: when is wolf control justified? Wildlife Society Bulletin 13:449-458.

Van Ballenberghe, V. 1981. Population dynamics of wolves in the Nelchina Basin, southcentral Alaska. Pages 1246-1258 *in* J. A. Chapman and D. Pursley, technical coordinators. Proceedings of the Worldwide Furbearer Conference, Worldwide Furbearer Conference, Frostburg, Maryland, USA.

_____. 1983. Extraterritorial movements and dispersal of wolves in southcentral Alaska. Journal of Mammalogy 64:168-171.

Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring of a recovering gray wolf population in Wisconsin, 1979-1991. Pages147-156 *in* L.N. Carbyn, S.H. Fritts, and D.R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35, University of Alberta, Edmonton.

Fig. 1. The Kenai Peninsula in southcentral Alaska, and location of the Kenai National Wildlife Refuge (KNWR) and Game Management Subunit (GMS) 15A.

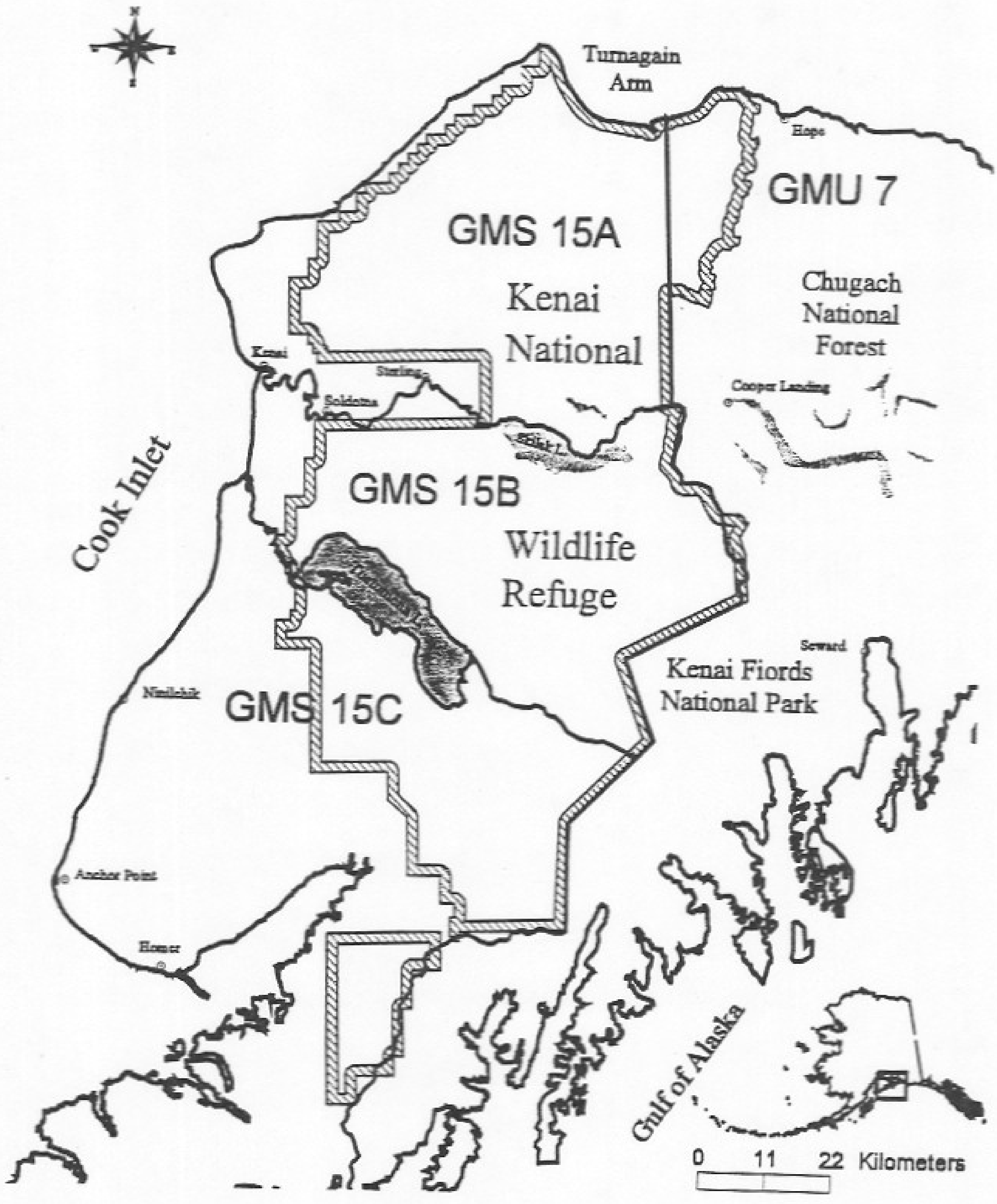

Turnagain Arm
Hope
GMU 7
GMS 15A
Kenai National
Chugach National Forest
Kenai
Sterling
Soldotna
Cooper Landing
Cook Inlet
GMS 15B
Wildlife Refuge
Seward
Kenai Fiords National Park
Ninilchik
GMS 15C
Anchor Point
Homer
Gulf of Alaska
0 11 22 Kilometers

Fig. 2. Winter wolf pack territory sizes for Bear Lake pack (BLP), Skilak pack (SKILAK), Point Possession pack (PPP), Swanson River pack (SRP), Moose River Flats pack (MRF), and Elephant Lake pack (ELP) on the Kenai National Wildlife Refuge, Alaska during 1982/83-1992/93.

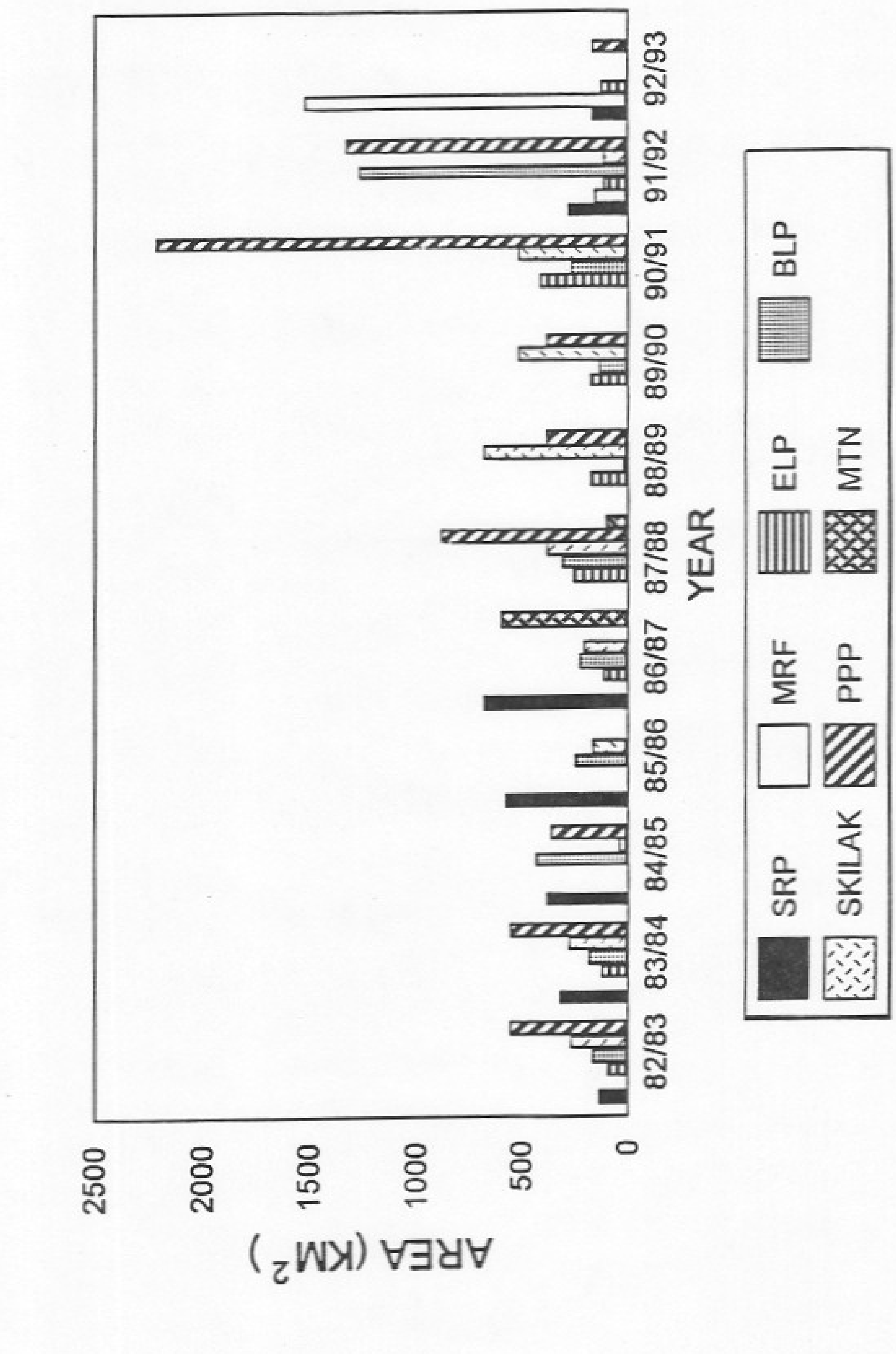

AREA (KM²)
2500
2000
1500
1000
500
0
82/83
83/84
84/85
85/86
86/87
87/88
88/89
89/90
90/91
91/92
92/93
YEAR
SRP
MRF
ELP
BLP
SKILAK
PPP
MTN

Fig. 3. Probability of dispersal by age of wolf (pup, juvenile, adult) in relation to annual harvest in GMS 15A on the Kenai Peninsula, Alaska, during 1982/83-1992/93.

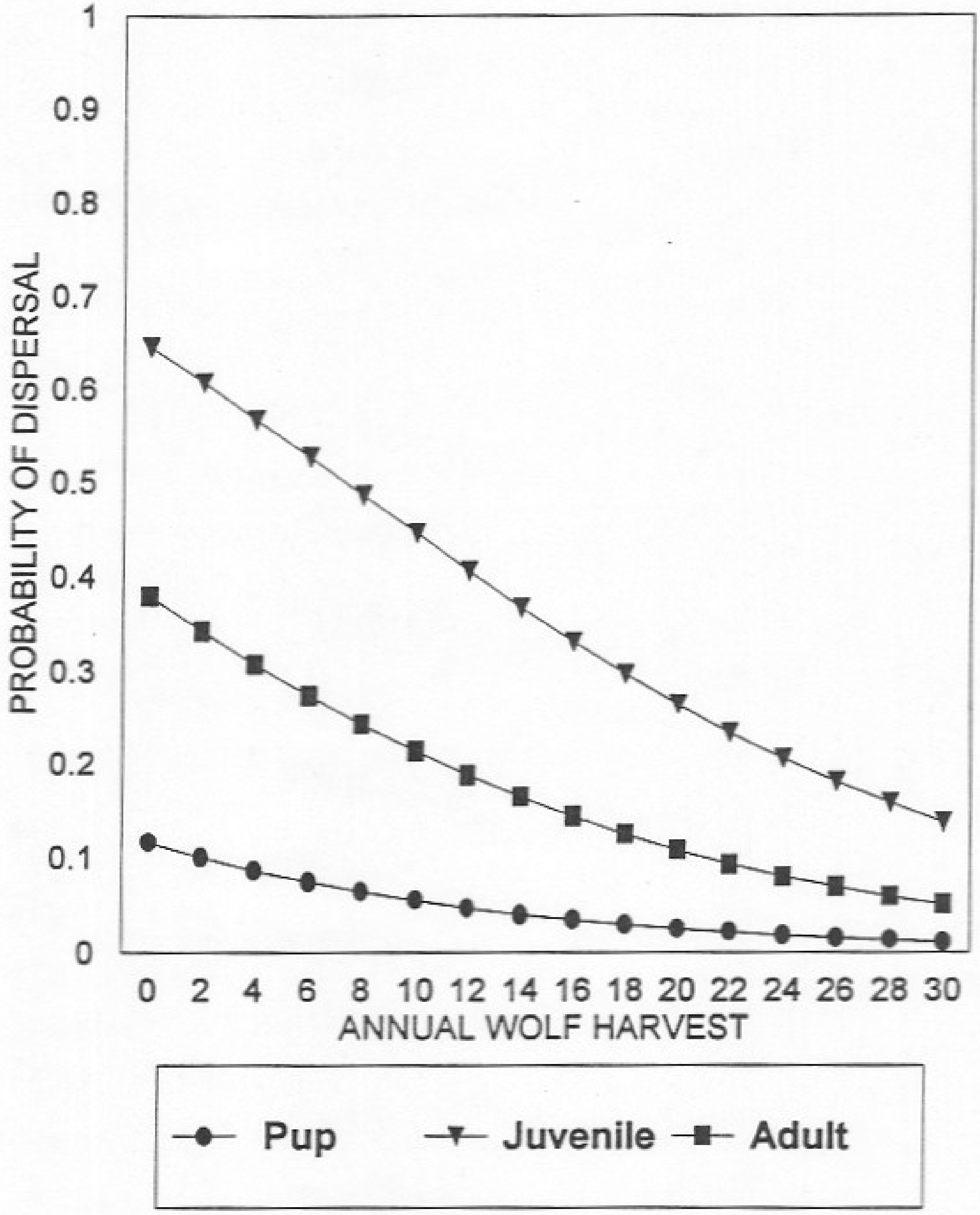

PROBABILITY OF DISPERSAL
ANNUAL WOLF HARVEST
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Pup
Juvenile
Adult

Table 1. Wolf density, pack and territory size, harvest, and dispersal rates in GMS 15A on the Kenai National Wildlife Refuge, Alaska during 1982/83-1992/93.

		Density[b]	Pack size			Pack territory size (km^2)[c]				
	Collared	(wolves/							%	%
Year	wolves[a]	1,000 km^2)	n	$\bar{x}$	SE	n	$\bar{x}$	SE	harvested[d]	dispersed[e]
1982/83	37	13.5	5	8.0	1.38	5	239.0	84.00	60.9	11.1
1983/84	27	17.0	5	10.0	1.18	5	289.1	74.27	46.5	9.5
1984/85	18	14.0	4	10.5	2.63	4	300.2	90.00	64.6	0.0
1985/86	12	9.4	5	5.6	0.68	3	326.0	123.85	71.2	16.7
1986/87	10	12.9	6	6.3	0.67	5	361.2	113.54	26.5	16.7
1987/88	14	12.3	6	6.0	1.12	5	382.5	131.99	20.5	0.0
1988/89	14	13.7	4	10.2	2.17	4	312.9	140.72	12.8	7.1
1989/90	17	13.7	4	10.2	1.89	4	297.6	88.91	10.6	16.7
1990/91	19	14.1	4	10.5	1.94	4	851.4	457.64	8.3	50.0
1991/92	21	14.3	6	7.2	1.25	6	537.2	240.15	4.1	62.5
1992/93	21	12.9	5	7.4	1.50	4	490.6	342.44	18.2	22.5

[a]Wolves monitored with functional radiocollars.
[b]Minimum population estimate divided by the census area (GMS 15A = 3,416 km^2).
[c]Territory size in winter (1 October-30 April) from Appendix 4.
[d]Percent of wolves harvested (Alaska Department of Fish and Game sealing records) from minimum wolf population estimate.
[e]Percent of radiocollared wolves that dispersed.

Table 2. Correlations between territory size and pack size and previous year's pack size in GMS15A on the Kenai National Wildlife Refuge, Alaska during 1982/83-1992/93.

Pack	Territory and pack size			Territory and previous year's pack size		
	r	df	*P*	*r*	df	*P*
Point Possession	0.15	8	0.702	0.10	7	0.812
Elephant Lake	0.41	8	0.271	0.51	7	0.196
Skilak Lake	0.20	9	0.572	0.31	8	0.410
Swanson River	0.68	6	0.095	0.83	4	0.084
Bear Lake	0.54	9	0.106	0.78	8	0.012
All packs	0.22	48	0.132	0.27	42	0.077

Table 3. Correlations between harvest and territory size and pack size of wolves in GMS 15A on the Kenai National Wildlife Refuge, Alaska during 1982/83-1992/93.

	Harvest and territory			Harvest and pack size		
Pack	*r*	df	*P*	*r*	df	*P*
Point Possession	-0.40	8	0.285	0.24	10	0.471
Elephant Lake	-0.43	8	0.247	-0.40	9	0.256
Skilak Lake	-0.54	9	0.108	-0.05	9	0.885
Swanson River	-0.06	6	0.894	-0.05	7	0.900
Bear Lake	-0.25	9	0.489	-0.06	10	0.867
All packs	-0.23	48	0.110	0.09	50	0.520

Appendix 1. Wolves trapped in summer and darted in winter on the Kenai National Wildlife Refuge, Alaska from 1982/83 - 1992/93.

Year	Previously captured[a]	Trapped	Darted
1982-83	4 (2 F, 2 M)	0 (0 F, 0 M)	33 (15 F, 18 M)
1983-84	14 (9 F, 5 M)	2 (1 F, 1 M)	11 (4 F, 7 M)
1984-85	12 (9 F, 3 M)	3 (1 F, 2 M)	3 (1 F, 2 M)
1985-86	6 (4 F, 2 M)	2 (2 F, 0 M)	4 (4 F, 0 M)
1986-87	4 (1 F, 3 M)	5 (3 F, 2 M)	1 (0 F, 1 M)
1987-88	8 (4 F, 4 M)	4 (1 F, 3 M)	2 (1 F, 1 M)
1988-89	10 (7 F, 3 M)	1 (0 F, 1 M)	3 (2 F, 1 M)
1989-90	8 (4 F, 4 M)	4 (1 F, 3 M)	5 (3 F, 2 M)
1990-91	10 (4 F, 6 M)	5 (1 F, 4 M)	4 (3 F, 1 M)
1991-92	12 (6 F, 6 M)	3 (1 F, 2 M)	6 (4 F, 2 M)
1992-93	15 (6 F, 9 M)	0 (0 F, 0 M)	6 (2 F, 4 M)

[a] Wolves darted or trapped previously, and monitored that year.

Appendix 2. Observed pack size, and yearly wolf population estimate in GMS 15A on the Kenai National Wildlife Refuge, Alaska, during 1982/83 -1992/93.

Pack[a]	1982-3	1983-4	1984-5	1985-6	1986-7	1987-8	1988-9	1989-0	1990-1	1991-2	1992-3
BLP	6	11	6	5	4	3	4	6	11	12	6
SKI	13	7	16	4	6	8	14	9	5	7	
PPP	8	14	14	6	5	8	12	11	12	9	4
SRP	5	9	6	8	8	8				3	7
ELP	8	9		5	7	7	11	15	14	6	14
MRF										6	7
MTN					8	3					
Population Estimate[b]	46	58	48	32	44	42	47	47	48	49	44

[a] BLP = Bear Lake pack

SKI = Skilak Lake pack

PPP = Point Possession pack

SRP = Swanson River pack

ELP = Elephant Lake pack

MRF = Moose River Flats pack

MTN = Mountain pack

[b] Estimate derived from number of wolves in packs multiplied by 1.15 correction factor for lone wolves and pairs within GMS 15A; Pack counts include wolves known to have been harvested before visual pack counts were made.

Appendix 3. Observed pack sizes for radioed wolves in GMS 15B on the Kenai National Wildlife Refuge, Alaska from 1982 - 1993.

Pack[a]	1982-3	1983-4	1984-5	1985-6	1986-7	1987-8	1988-9	1989-0	1990-1	1991-2	1992-3
BCP	2										4
MTN				3						7	
QCP	2	4									
15B										2	9
KIL	4										
BIP				16							

[a] BCP = Bear Creek pack

MTN = Mountain pack

QCP = Quartz Creek pack

15B = 15B pack

KIL = Killey River pack

BIP = Big Indian pack

Appendix 4. Wolf pack winter territory size, minimum pack size, and pack density on the Kenai National Wildlife Refuge, Alaska from 1982/83-1992/93.

Pack	Year	Territory size (km^2)	Relocations (*n*)	Pack size	Wolves / 1,000 km^2
Bear Lake	1982-83	161.0	18	6	37.3
	1983-84	181.7	32	11	60.5
	1984-85	431.3	12	6	13.9
	1985-86	244.8	30	5	20.4
	1986-87	220.3	15	4	18.2
	1987-88	305.8	14	3	9.8
	1988-89	22.6[a]	13	4	
	1989-90	129.9	22	6	46.2
	1990-91	266.4	36	11	41.3
	1991-92	1263.2	15	12	9.5
	1992-93			6	
Skilak Lake	1982-83	263.8	21	13	49.3
	1983-84	278.9	26	7	25.1
	1984-85	34.5[a]	9	16	
	1985-86	164.0	11	4	24.4
	1986-87	207.8	9	6	28.9

Appendix 4. Continued.

Pack	Year	Territory size (km^2)	Relocations (n)	Pack size	Wolves / 1,000 km^2
	1987-88	376.5	22	8	21.2
	1988-89	674.6	56	14	20.8
	1989-90	509.6	11	9	17.7
	1990-91	513.8	65	5	9.7
	1991-92	108.4	27	7	64.6
Pt. Possession	1982-83	553.9	18	8	14.4
	1983-84	549.6	55	14	25.5
	1984-85	355.4	17	14	39.4
	1985-86			6	
	1986-87			5	
	1987-88	878.5	38	8	9.1
	1988-89	377.1	25	12	31.4
	1989-90	377.6	14	11	29.1
	1990-91	2215.9	37	12	5.4
	1991-92	1321.2	23	9	6.8
	1992-93	160.7	16	4	24.9
Swanson River	1982-83	130.9	20	5	38.2

Appendix 4. Continued.

Pack	Year	Territory size (km^2)	Relocations (n)	Pack size	Wolves / 1,000 km^2
	1983-84	319.1	20	9	21.9
	1984-85	379.6	6	6	15.8
	1985-86	569.3	11	8	14.0
	1986-87	674.7	6	8	
	1987-88			8	
	1991-92	273.3	20	3	11.0
	1992-93	167.4	32	7	41.8
Elephant Lake	1982-83	85.5	15	8	93.6
	1983-84	116.1	10	9	77.5
	1985-86			5	
	1986-87	110.9	16	7	63.1
	1987-88	250.6	62	7	27.9
	1988-89	177.2	43	11	62.1
	1989-90	173.5	19	15	86.4
	1990-91	409.6	49	14	34.2
	1991-92	108.4	38	6	55.4

Appendix 4. Continued.

Pack	Year	Territory size (km²)	Relocations (*n*)	Pack size	Wolves / 1,000 km²
	1992-93	117.0	14	14	119.7
Mountain[b]	1986-87	592.5	6	8	13.5
	1987-88	101.3	24	3	29.6
	1991-92[b]	36.5[a]	4	7	
Bear Creek[b]	1982-83	333.1	10	2	6.0
	1983-84	65.5[a]	4		
	1992-93	311.3	10	4	12.8
Quartz Creek[b]	1982-83	23.7[a]	4	2	
	1983-84	19.3[a]	5	4	
Killey River[b]	1982-83	67.7	6	4	59.1
15B[b]	1991-92	495.0	11	2	4.0
	1992-93	187.2	7	9	48.1
Moose Rvr Flats	1991-92	148.5	9	6	40.4
	1992-93	1517.4	29	7	4.6

[a] Excluded from density calculations because actual territory probably larger than data indicate.

[b] Wolf packs residing in GMS 15B or GMU 7.

Appendix 5. Estimates of wintering moose density (moose/km^2) in two recent burns and mature habitat in GMS15A on the Kenai Peninsula, AK from 1979-1995.

	47 Burn		69 Burn		Mature forest		Overall population	
Year	Density	80% CI	Density	80% CI	Density	80% CI	Estimate	80% CI
1979[a]	1.7	1.2 - 2.2			0.4	0.1 - 0.6	2589	1959 - 3220
1982[a]	1.3	1.0 - 1.6	4.4	2.7 - 6.0	0.7	0.3 - 1.1	4352	3267 - 5437
1987[b]	0.3	0.1 - 0.4	3.5	3.3 - 3.7	0.1	<0.1-0.3	2349	2175 - 2524
1990[b]	0.5	0.4 - 0.7	3.8	3.7 - 4.0	0.2	<0.1-0.4	3432	3114 - 3750
1995[b]	0.1	<0.1-0.2	1.5	1.1 - 2.0	0.2	<0.1-0.3	1585	1352 - 1817

[a]KNWR unpublished data using quadrat survey method from Evans et al. (1966).

[b]KNWR unpublished data using survey technique from Gasaway et al. (1986), with pooled variances.

Appendix 6. Age and sex composition, and proportion of radiocollared wolves that dispersed on the Kenai National Wildlife Refuge, Alaska during 1982-93.

	Monitored sample							Dispersers				
	No.	Sex		Age[c]			No.	Sex		Age		
Year[a]	radioed[b]	M	F	A	J	P	dispersed	M	F	A	J	P
1982/83	18	7	11	11	1	6	2	1	1	2	0	0
1983/84	21	7	14	4	3	14	2	1	1	1	1	0
1984/85	9	3	6	5	4	0	0					
1985/86	6	3	3	4	0	2	1	0	1	1	0	0
1986/87	6	4	2	5	1	0	1	1	0	0	1	0
1987/88	11	6	5	9	0	2	0					
1988/89	14	7	7	9	2	3	1	1	0	0	1	0
1989/90	12	8	4	7	4	1	2	2	0	1	1	0
1990/91	14	10	4	12	1	1	7	5	2	5	1	1
1991/92	16	9	7	13	1	2	10	6	4	10	0	0
1992/93	18	10	8	13	4	1	4	1	3	1	3	0

[a]Dispersal was calculated from 1 September to 31 August.

[b]Radiocollared wolves monitored >3 months were included in radioed sample.

[c]A=adult, J=juvenile, P=pup

Appendix 7. Wolf dispersal on the Kenai National Wildlife Refuge, Alaska from 1982-1993.

Year[a]	Wolf	Pack	Date[b]	Disposition
1982/83	M63	SRP	1/83	Joined with F71, reproduced.
1982/83	F71	PPP	1/83	Joined with M63, denned.
1983/84	F45	BLP	2/84	With Skilak pack on 2/84.
1983/84	M75	PPP	3/84	Radiocollar found in Cantwell, Alaska 8/86.
1985/86	F86	PPP	1/86	Killed by other wolves 5/86.
1986/87	M115	BLP	11/86	Radiocollar found in Homer, Alaska 5/87.
1988/89	M124	PPP	12/88	Harvested in Fairbanks, Alaska 1/90.
1989/90	M130	BLP	unknown	Dispersed south to 15B, 3/90.
1989/90	M138	ELP	3/90	Killed by PPP wolves in PPP territory.
1990/91	F144	BLP	2/91	Located in Palmer, Alaska 6/91.
1990/91	M131	ELP	4/91	Harvested in 15A, 11/93.
1990/91	M145	ELP	3/91	Harvested in Paxson, Alaska 3/92.
1990/91	M134	PPP	unknown	
1990/91	M137	SKILAK	4/91	With 15B Pack.
1990/91	F132	SKILAK	2/91	With M140 (PPP) 2/91-5/91, Formed SKI_LP pack.
1990/91	M140	PPP	5/91	With F132 (SKILAK) on 5/91, formed SKI_LP pack.
1991/92	F148	ELP	2/92	Left ELP, with M149 moved north to Chickaloon Creek
1991/92	M149	ELP	2/92	Left ELP, with F148 moved north to Chickaloon Creek
1991/92	M155	PPP	4/92	Illegally killed 9/93.

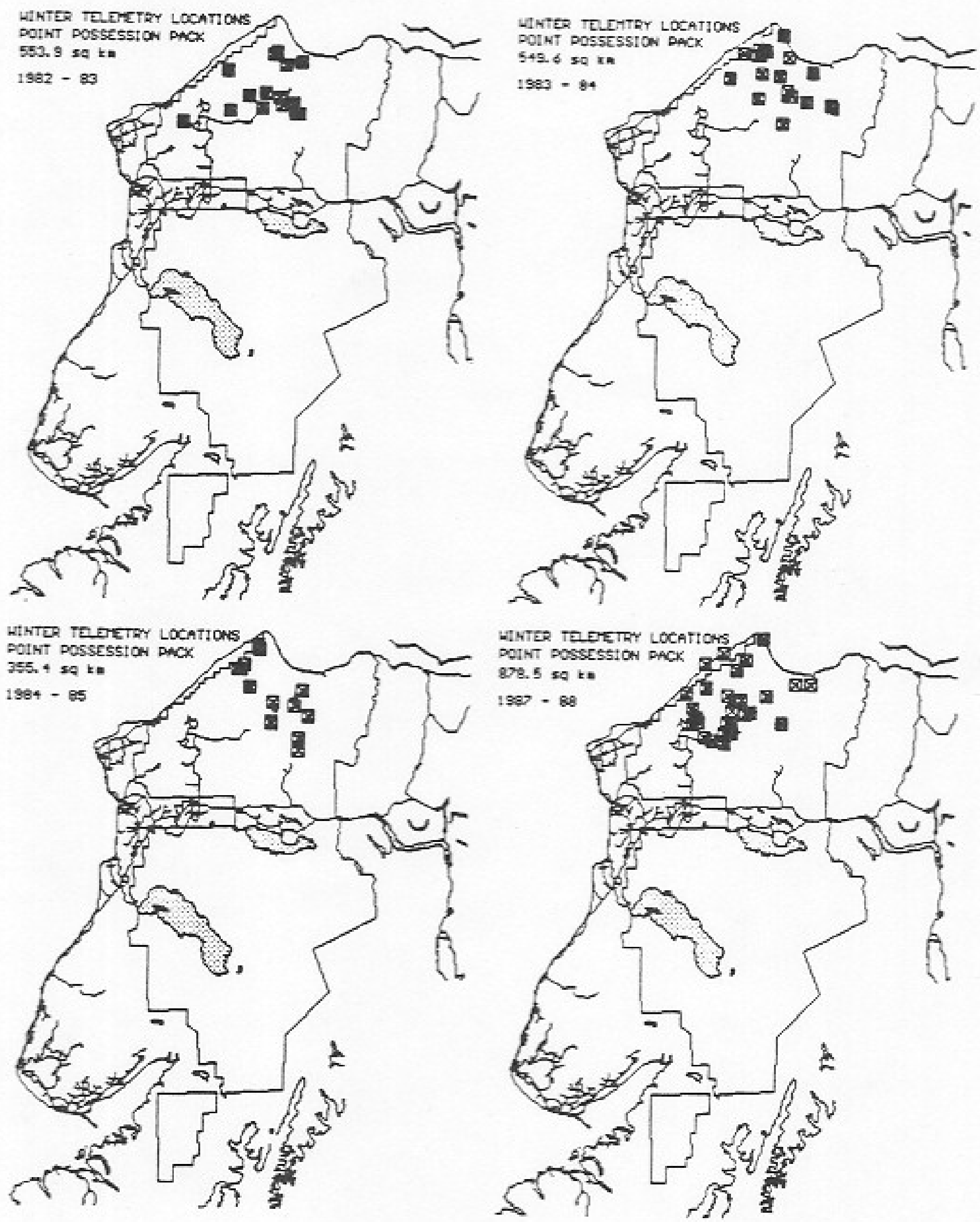
Appendix 7. Continued.

Year[a]	Wolf	Pack	Date[b]	Disposition
1991/92	M134	PPP	1/92	Joined F152 (SRP) on 1/92, formed SRP2 pack.
1991/92	M70	ELP	6/91	With F141 (SKILAK), formed new 15B pack
1991/92	F141	SKILAK	12/91	With M70 (ELP), formed new 15B pack
1991/92	M126	PPP	2/92	Joined ELP 2/92.
1991/92	M143	BLP	1/92	With F151 (of SKI) both moved to MNT pack.
1991/92	F151	SKILAK	1/92	With M143 (of BLP), both moved to MTN pack.
1991/92	F125	PPP	1/92	With M159 (MRF) 1/92 which formed the MRF pack then F125 dispersed from MRF with M159 to GMU 15B.
1992/93	M157	SKI_LP	4/93	Last radiolocation in GMU 7, 4/93.
1992/93	F154	PPP	4/93	Harvested south Caribou Lake
1992/93	F152	SRP2	6/93	Harvested with F162 (ELP) fall, 1993.
1992/93	F162	ELP	4/93	Harvested with F152 (SRP2) fall, 1993.

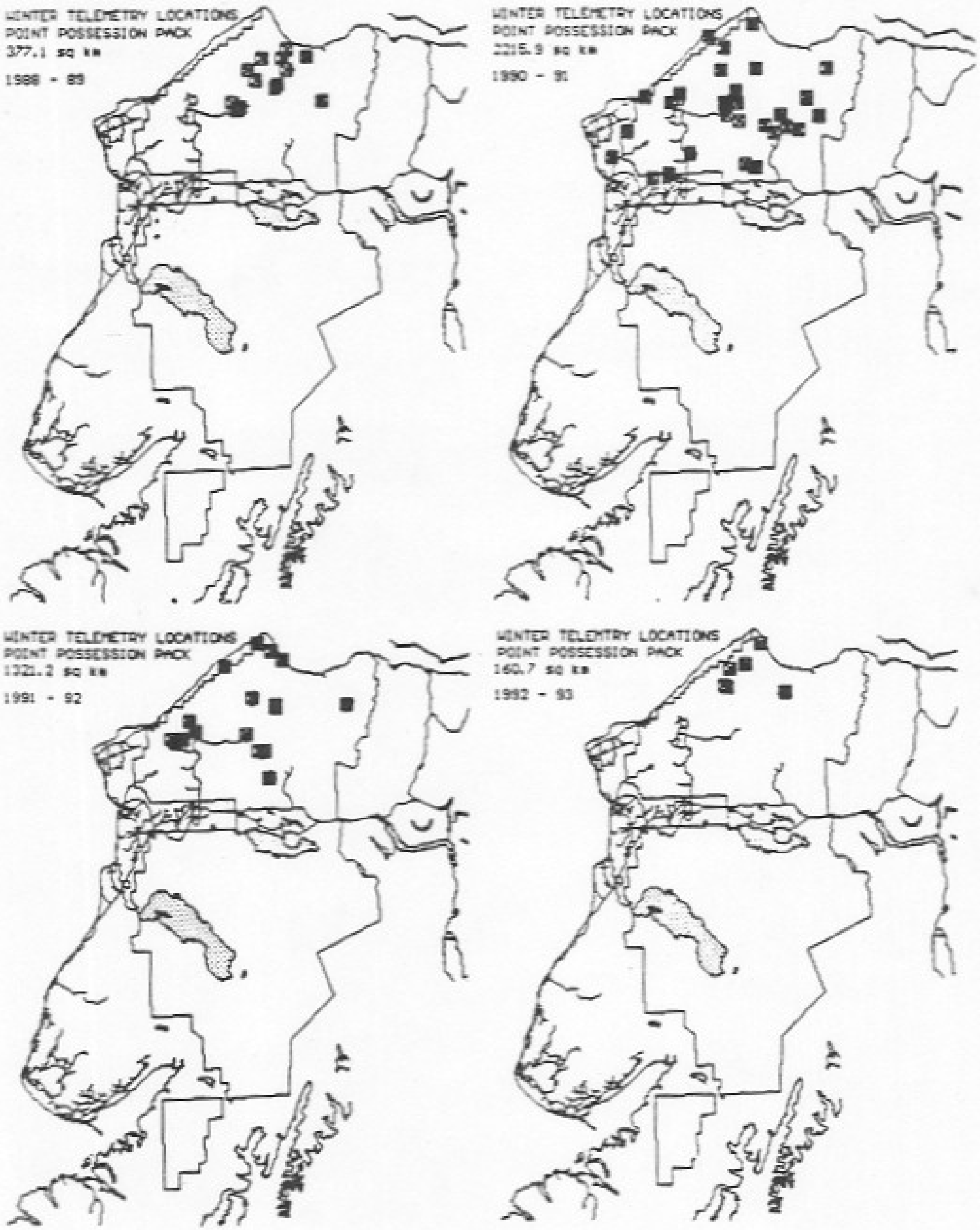
[a] Dispersal year calculated from 1 September through 31 August the following year.

[b] Last known date radiocollar was located within pack territory, and before dispersal movements were made.

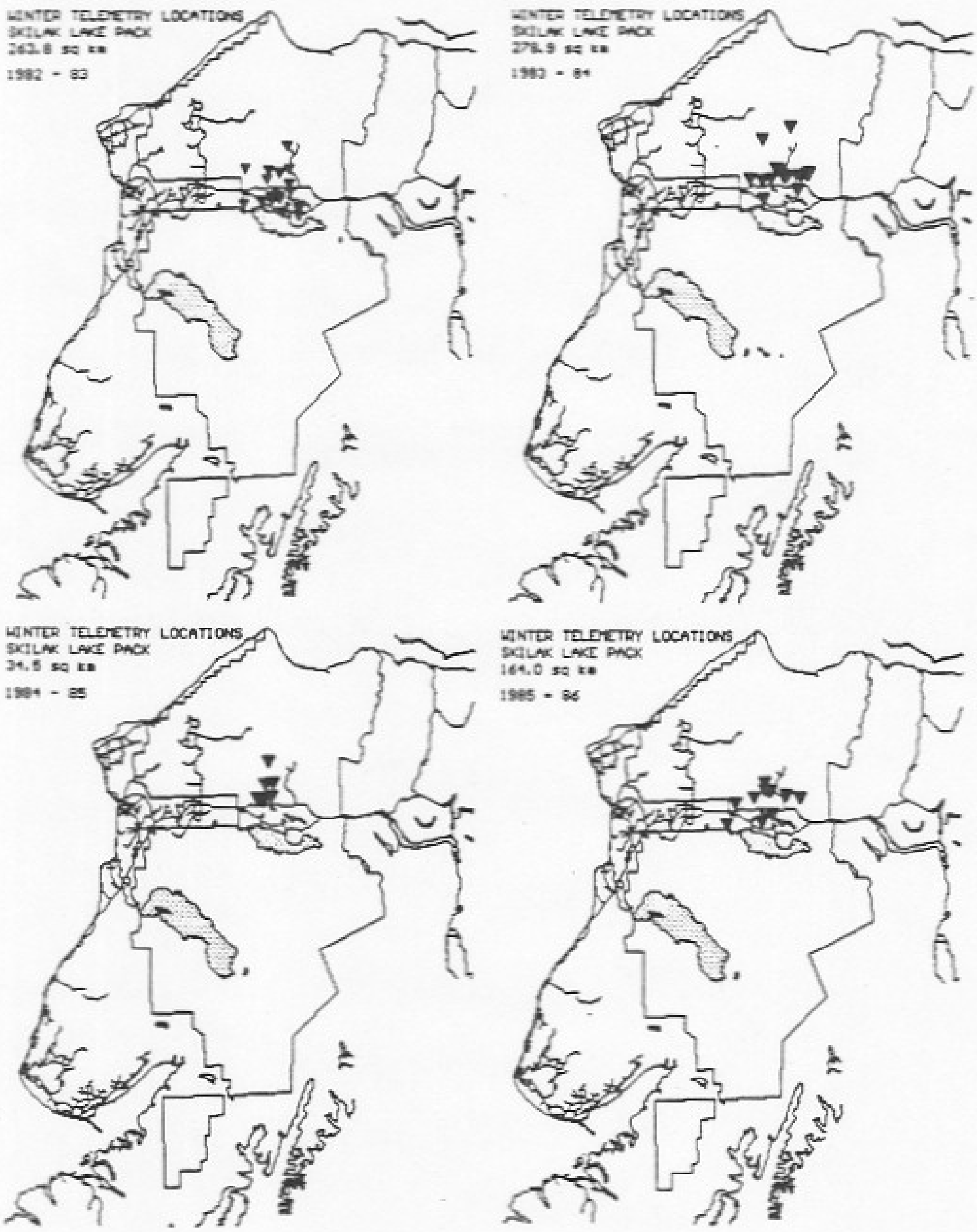
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



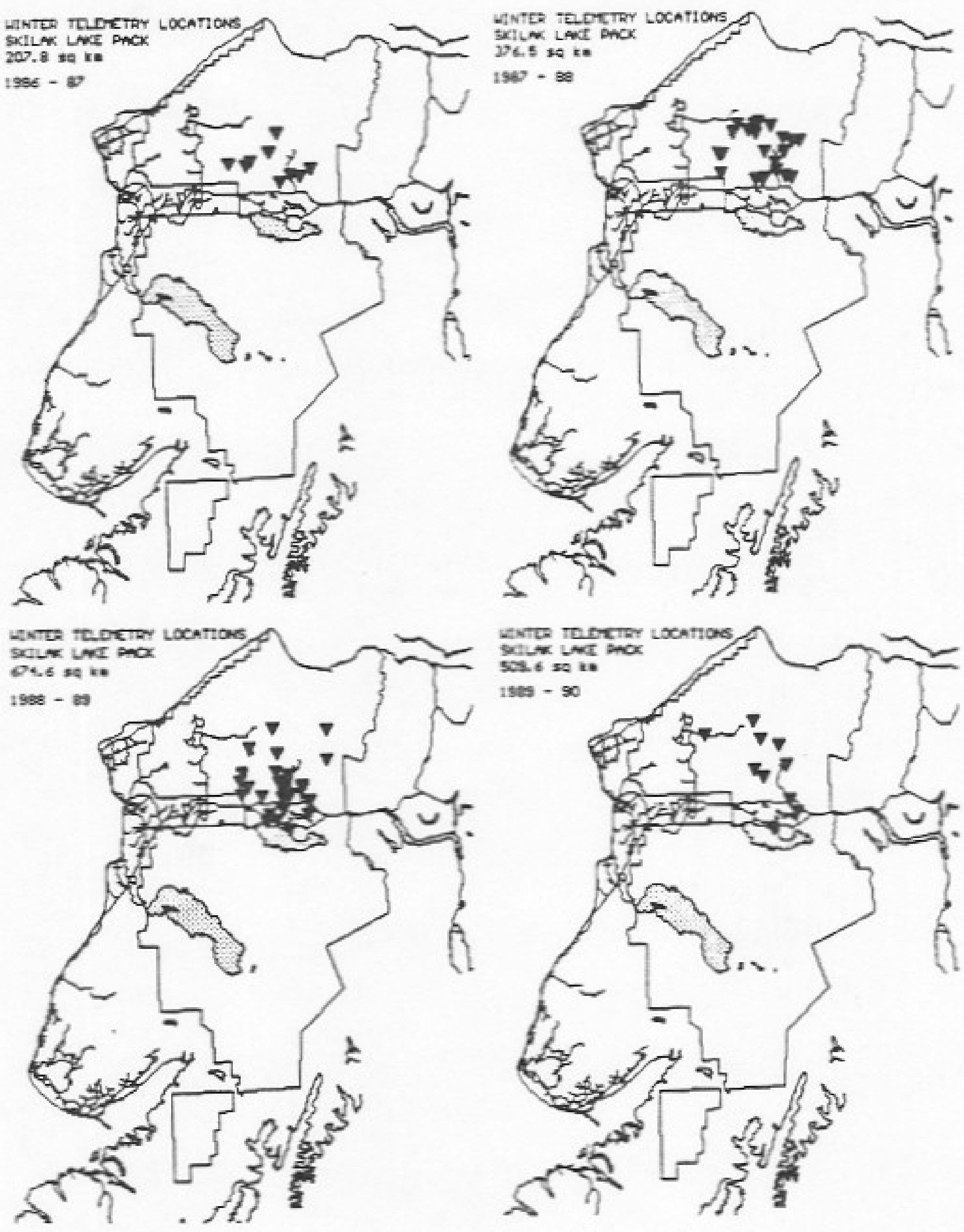
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



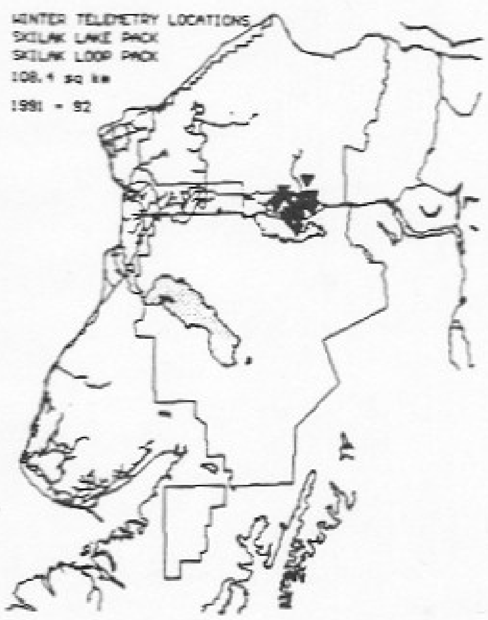
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



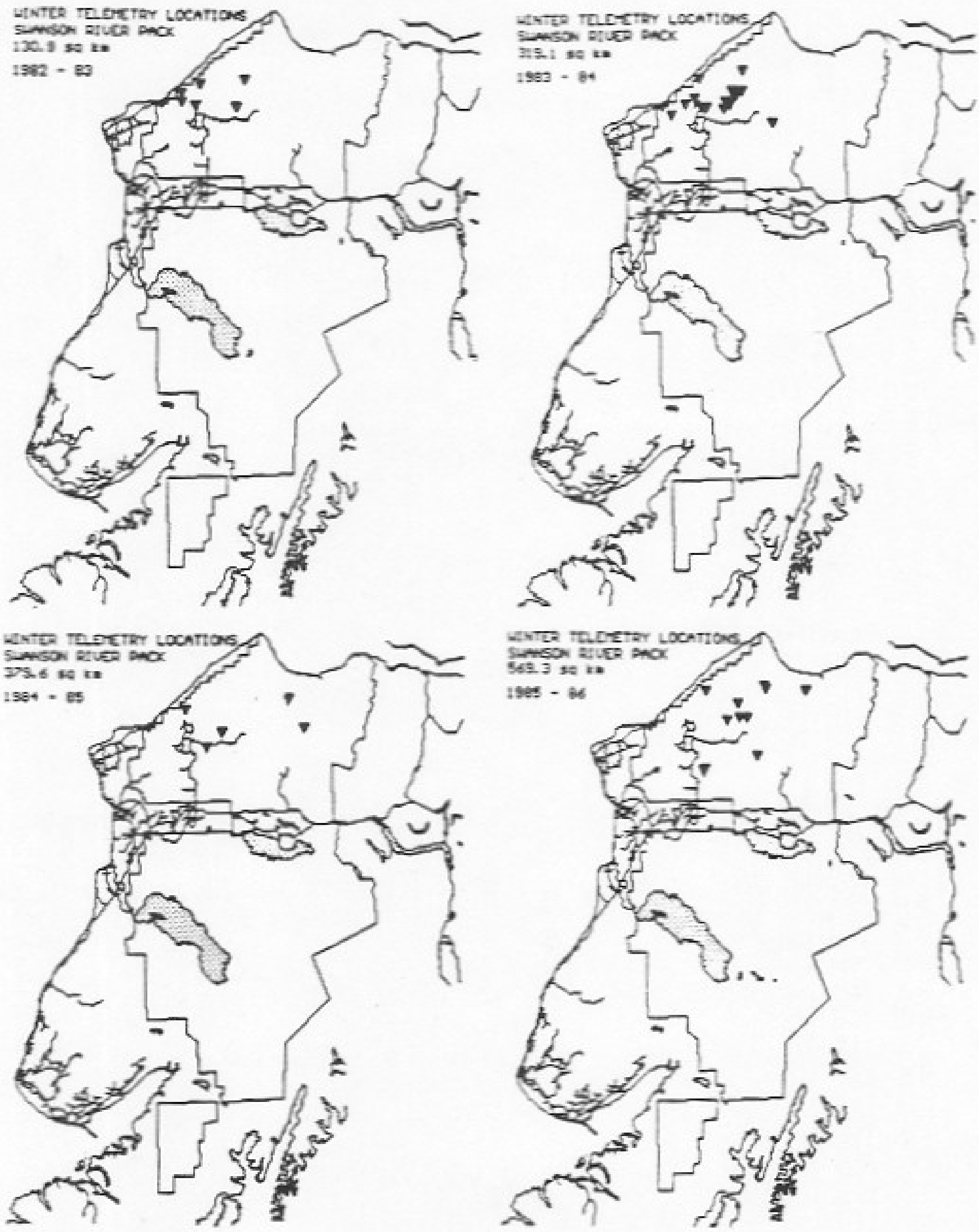
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



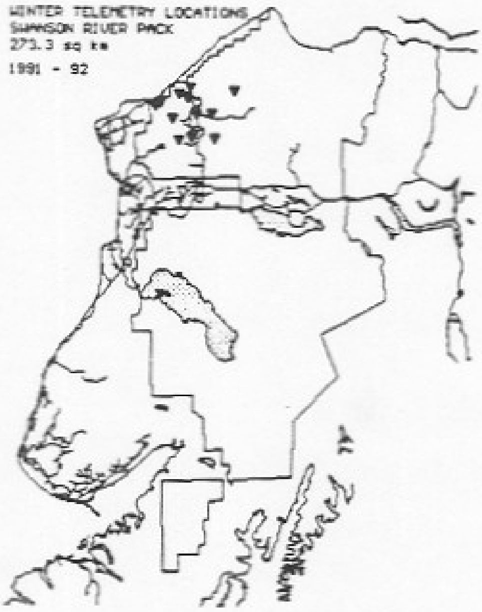
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



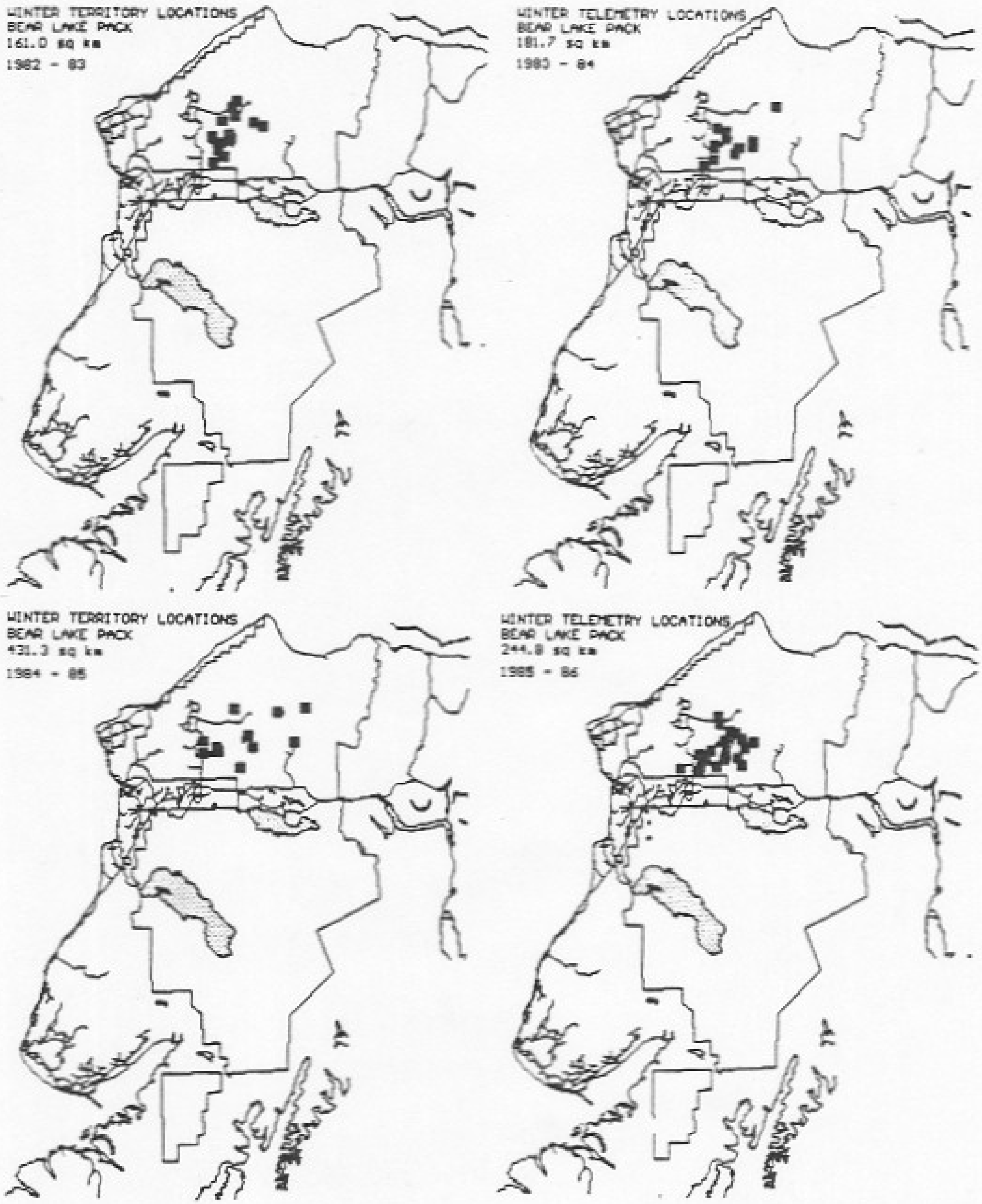
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



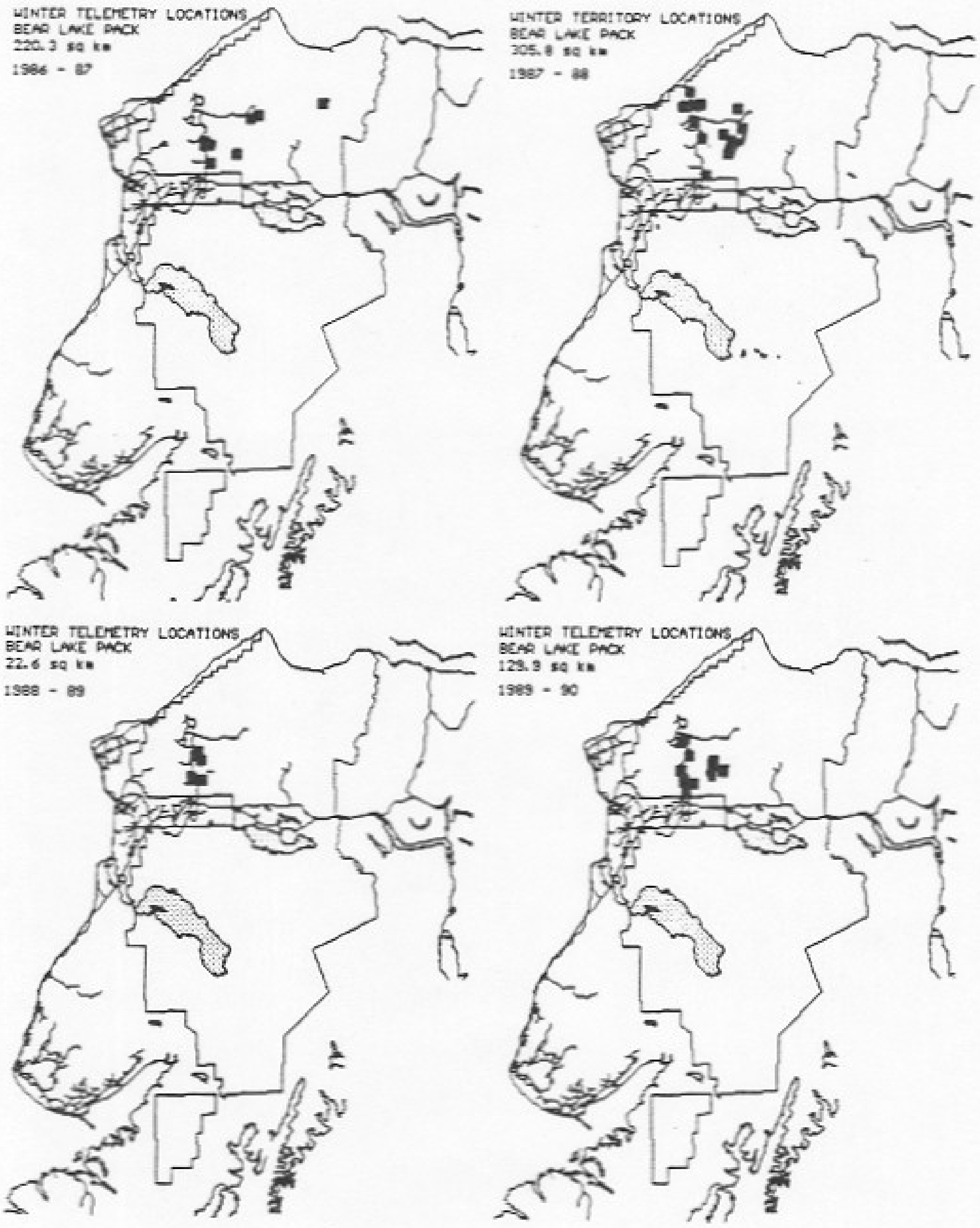
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



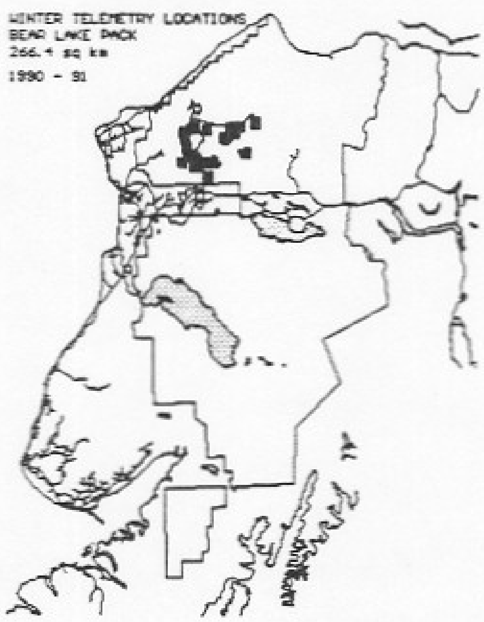
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

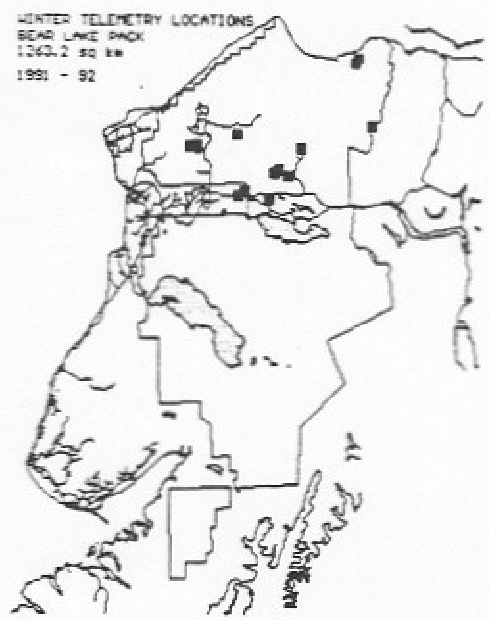


Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

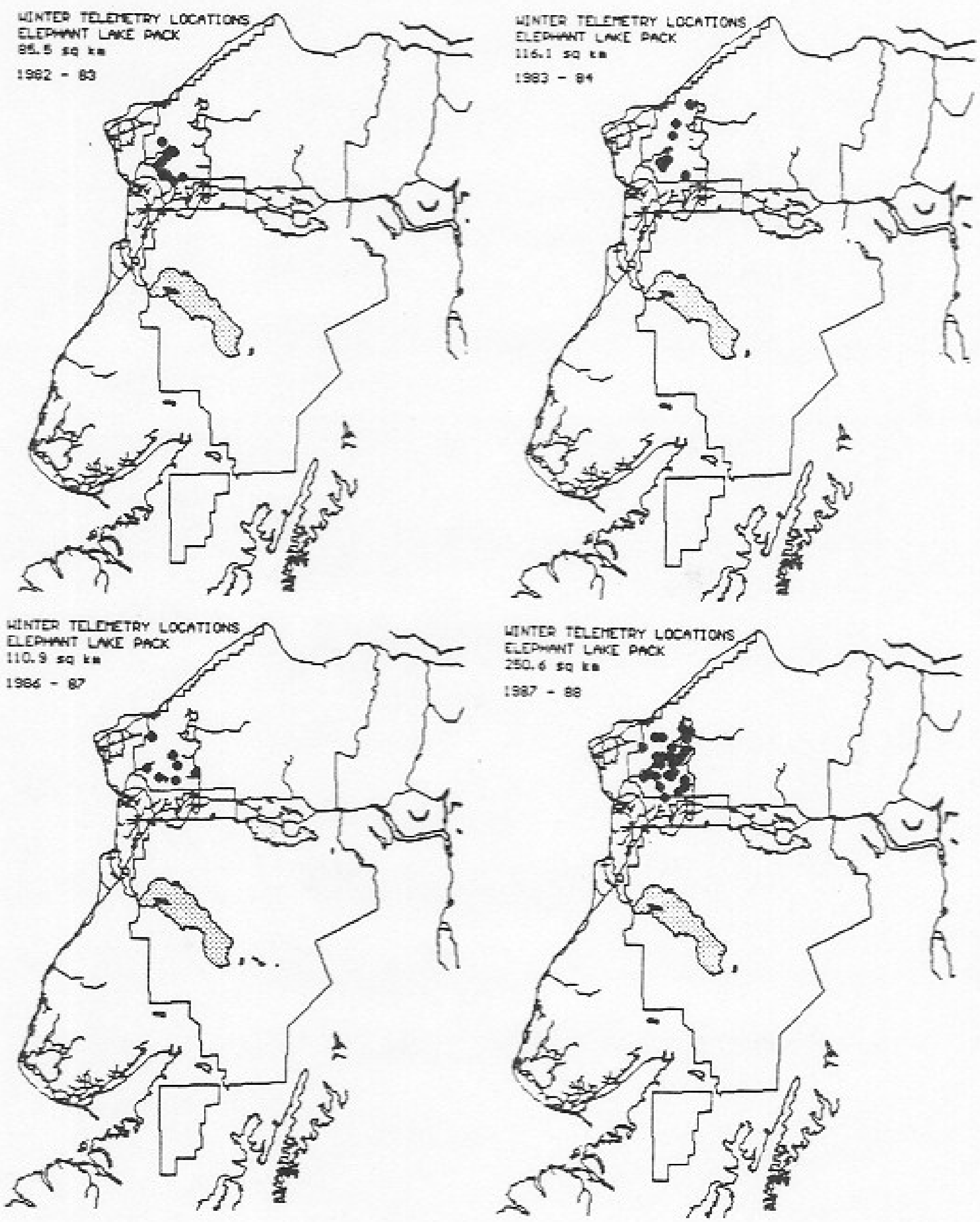


Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

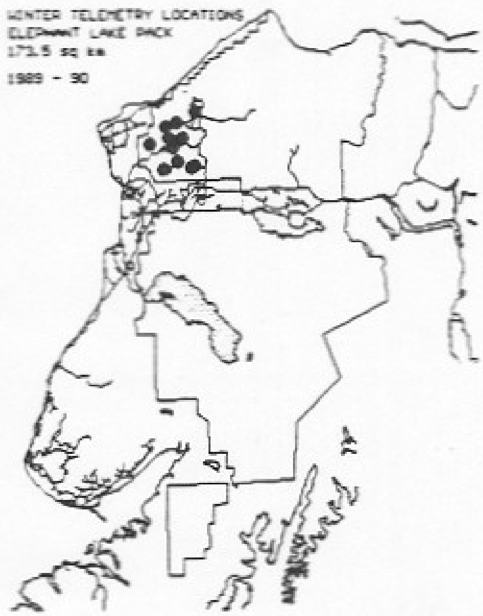




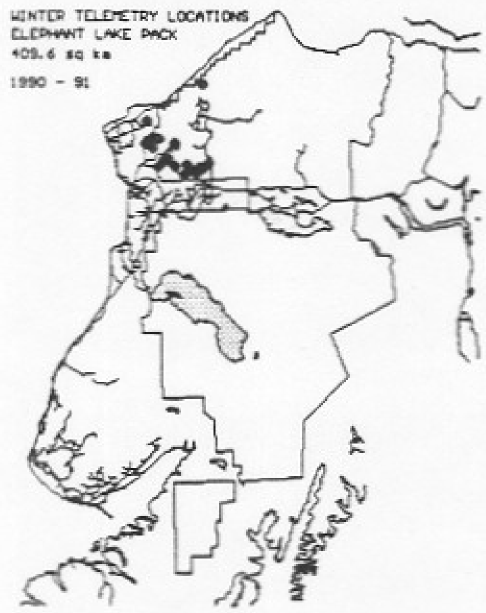
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

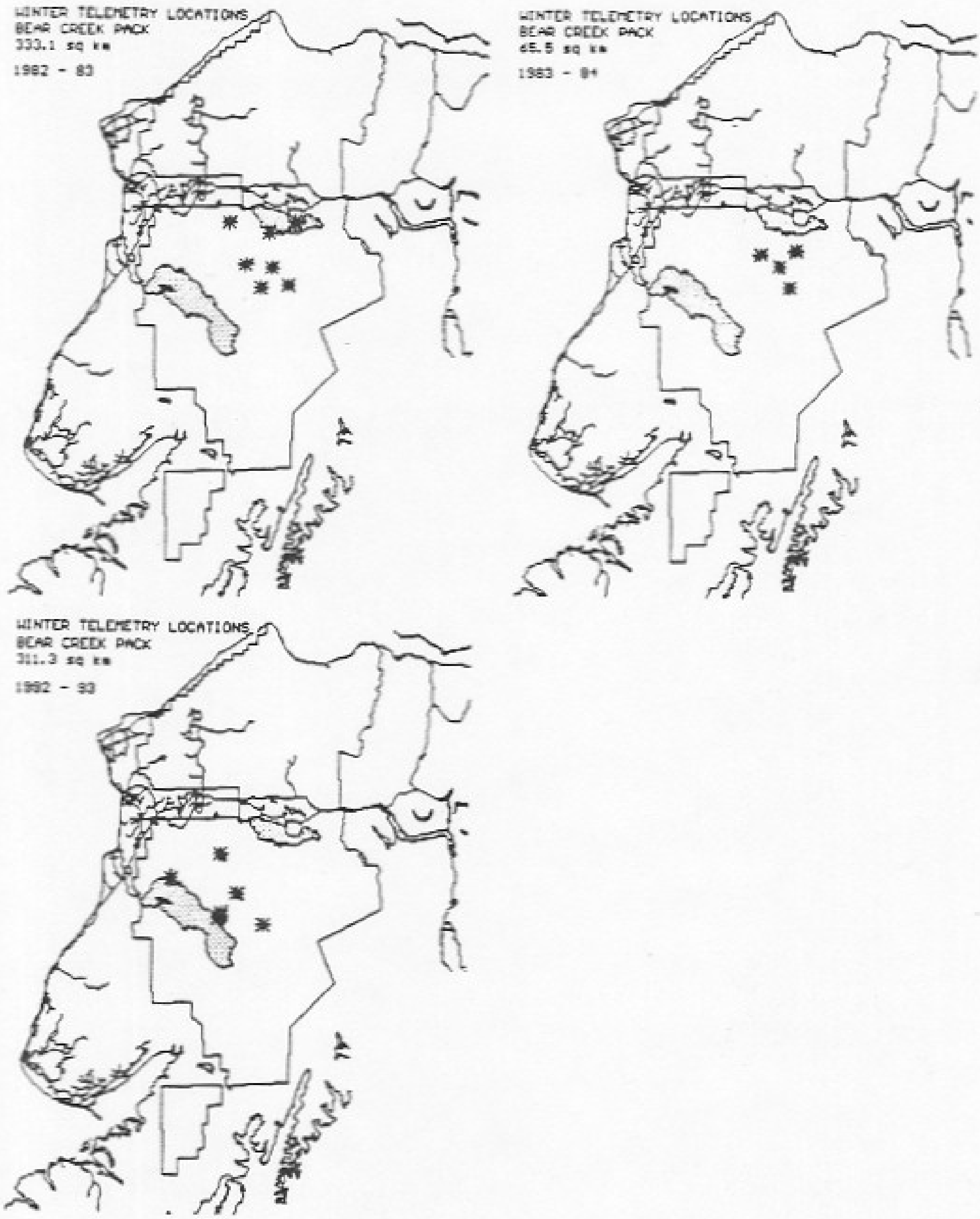


Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

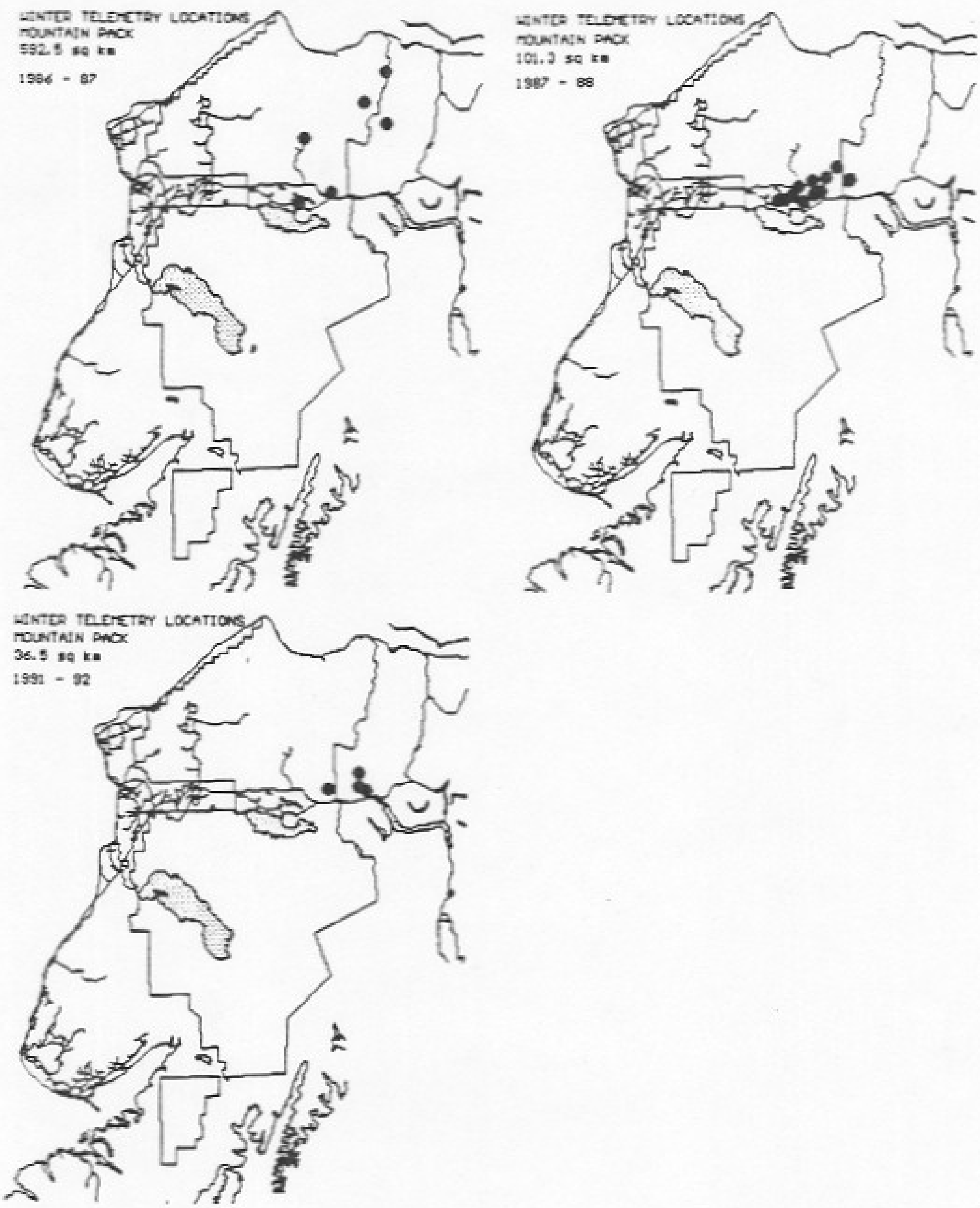


Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

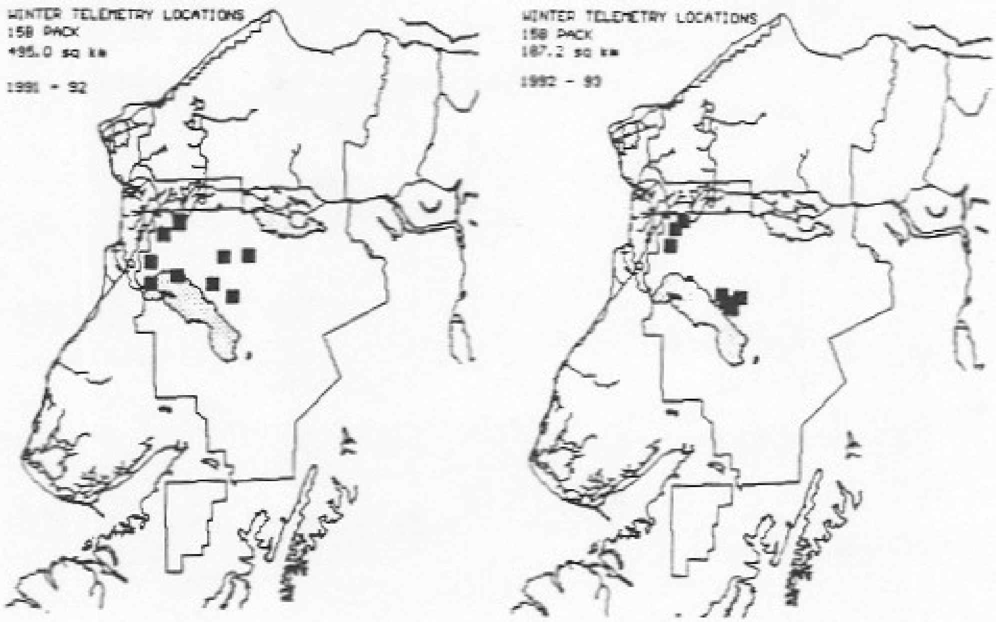
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

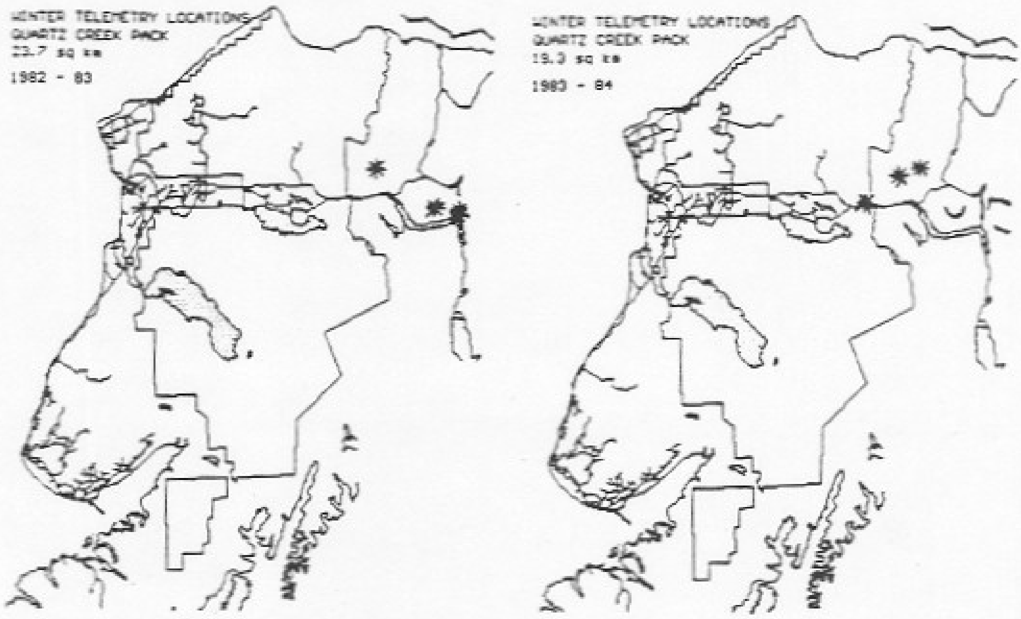


Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



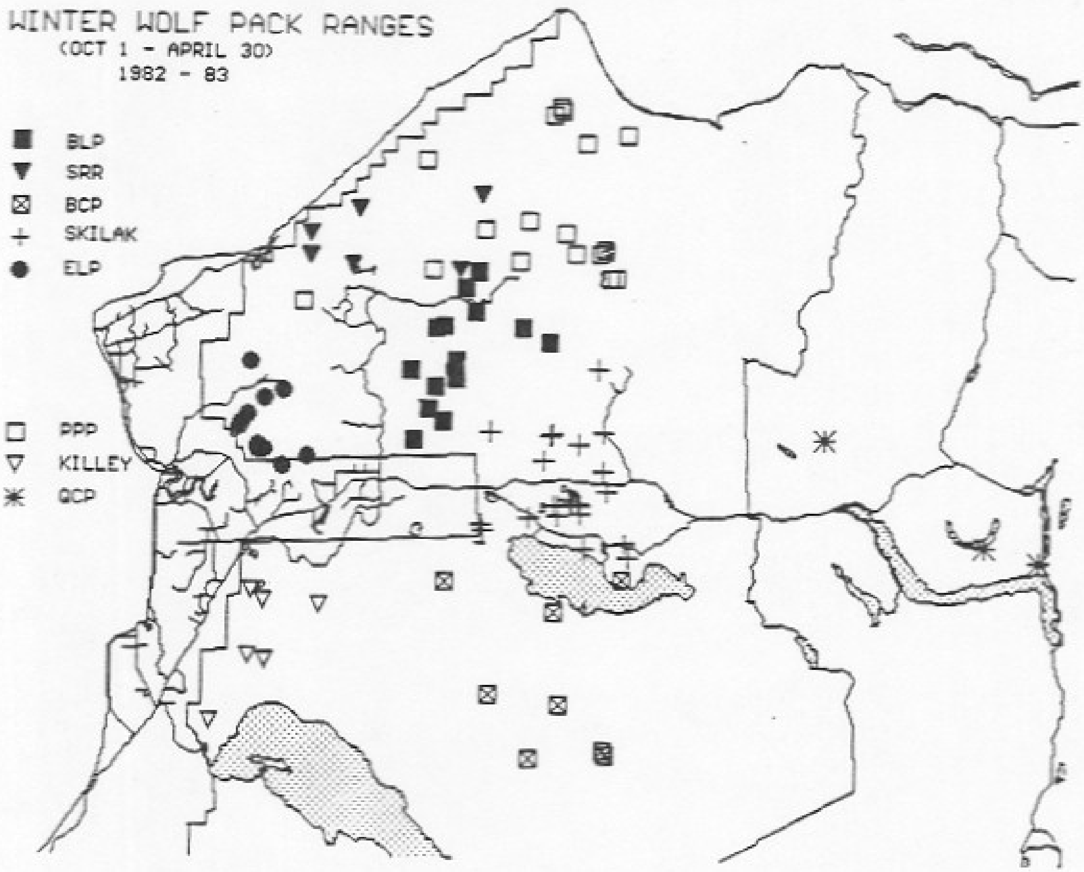
Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

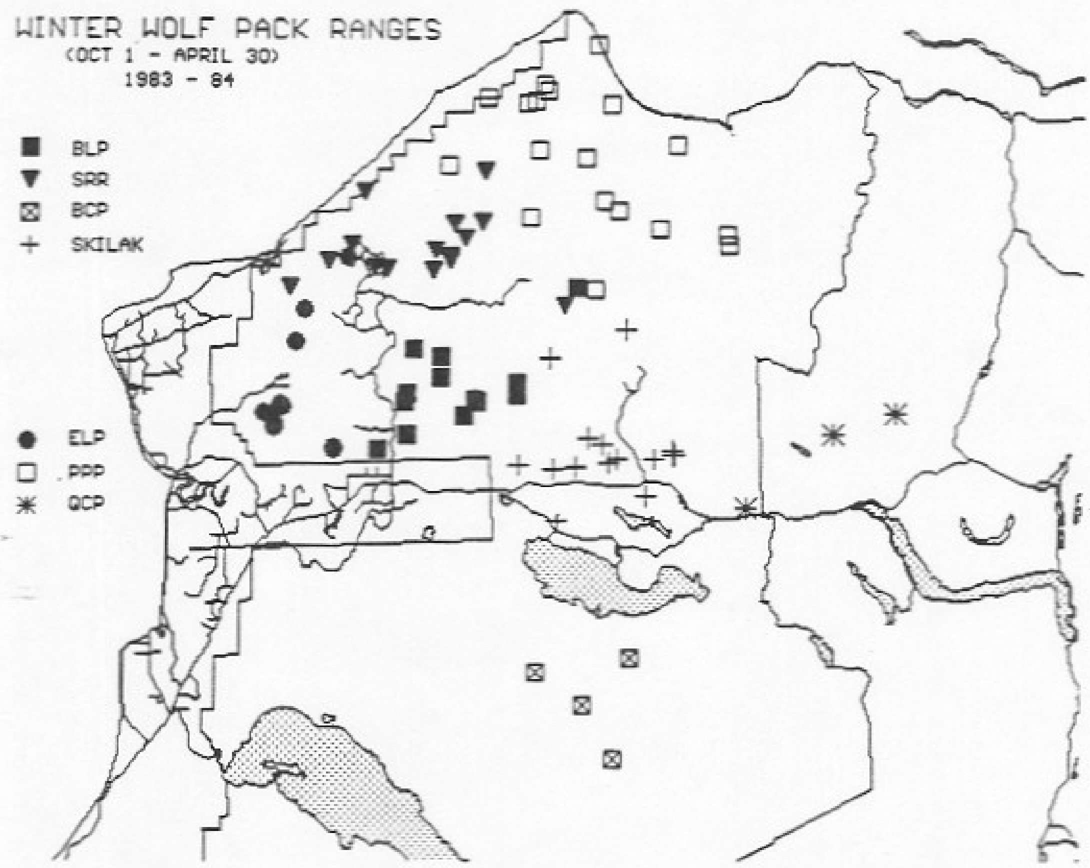


Appendix 8. Telemetry locations in winter for each pack monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.

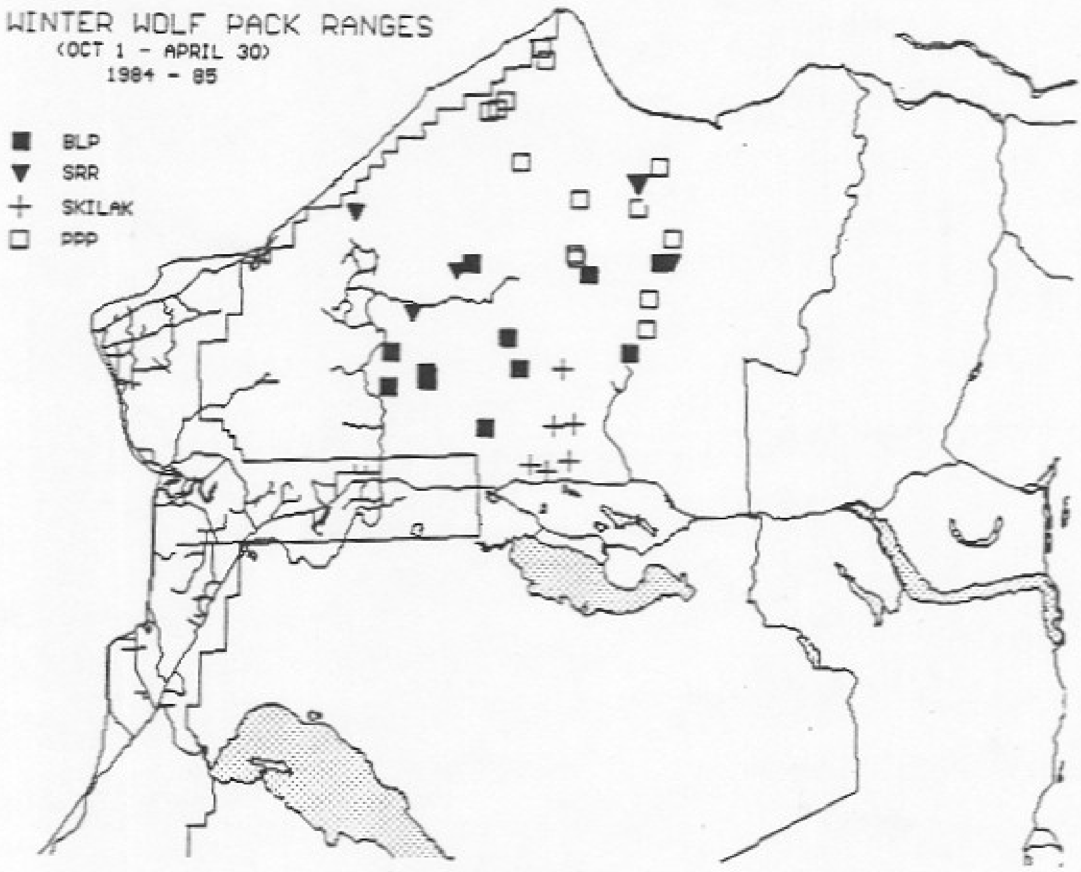
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



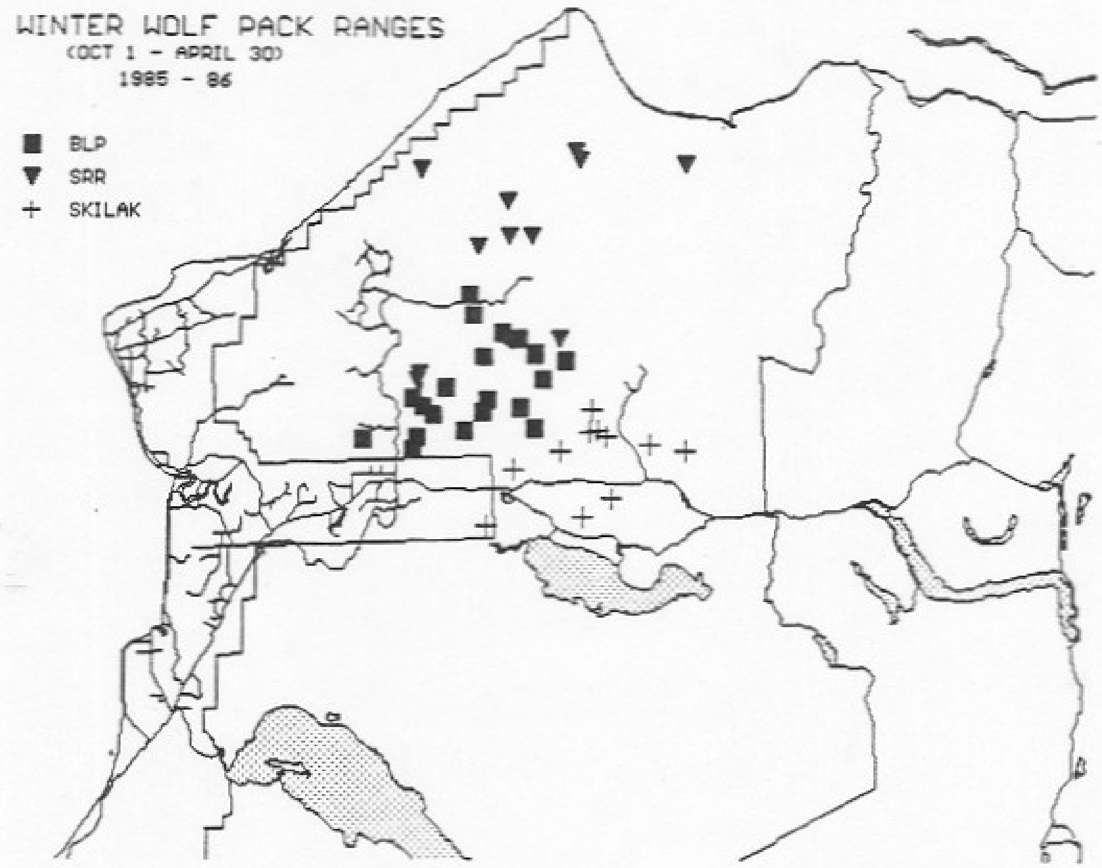
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



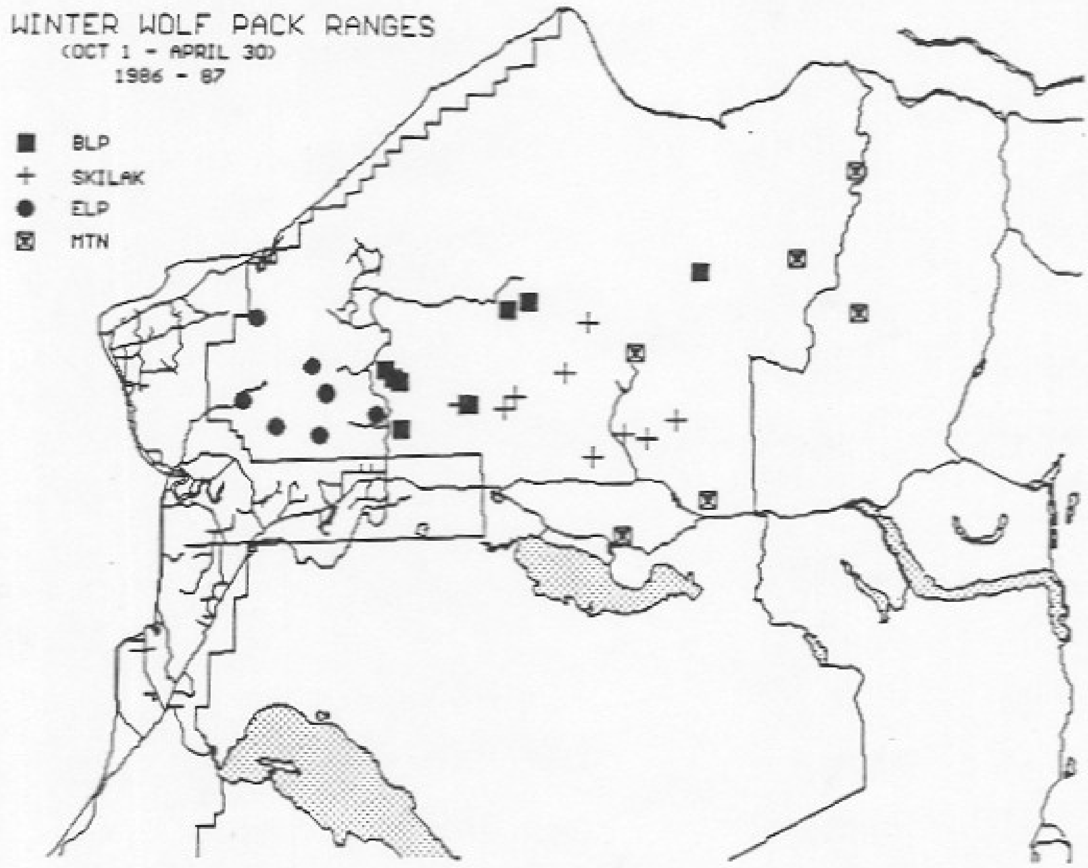
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



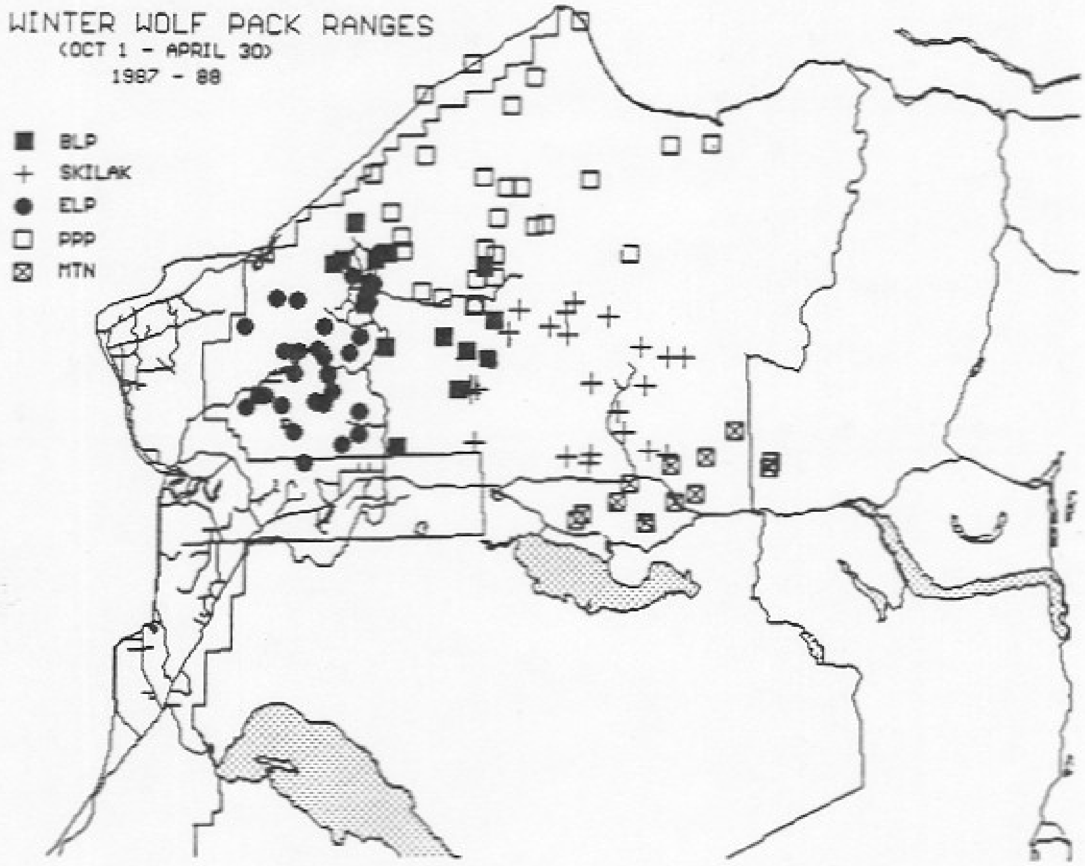
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



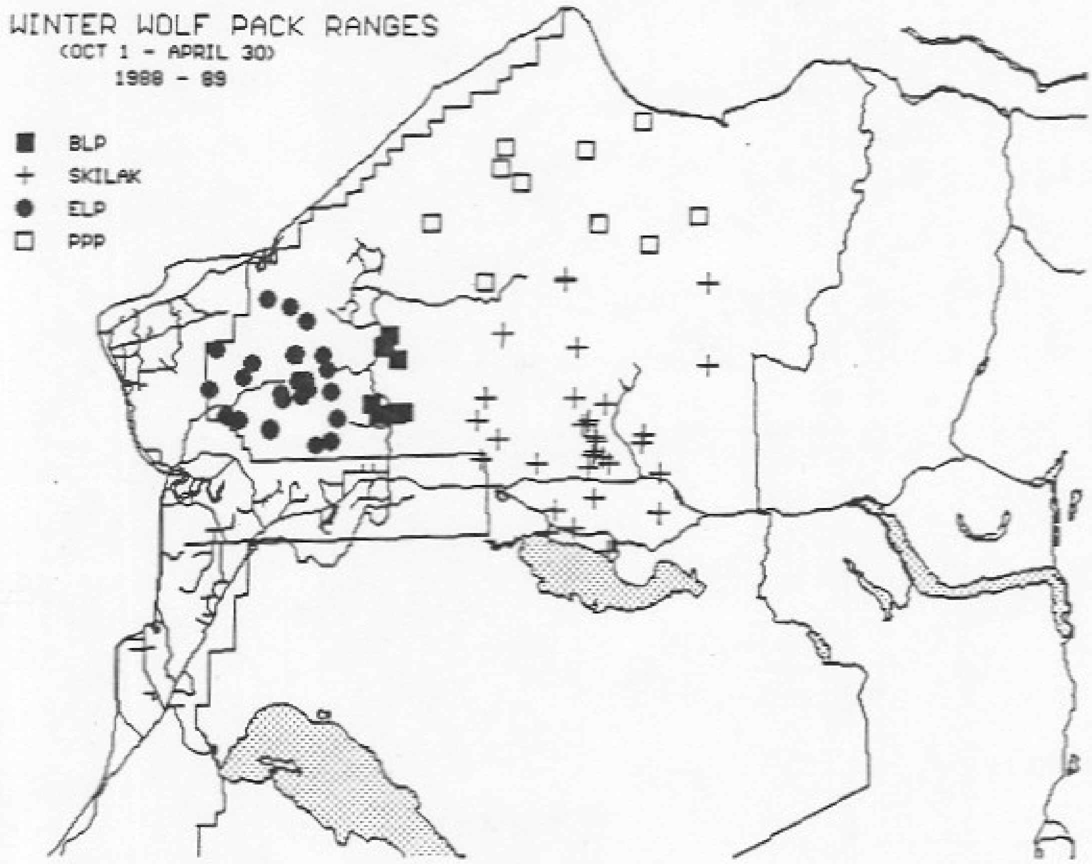
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



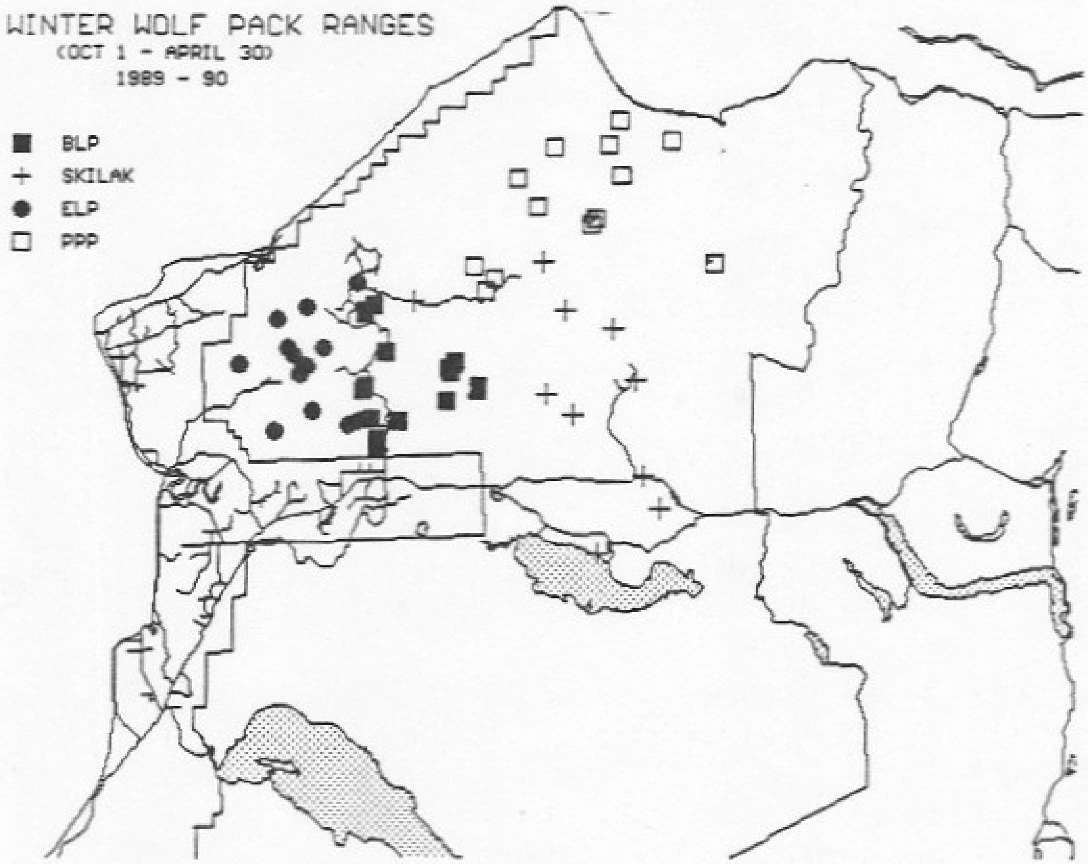
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



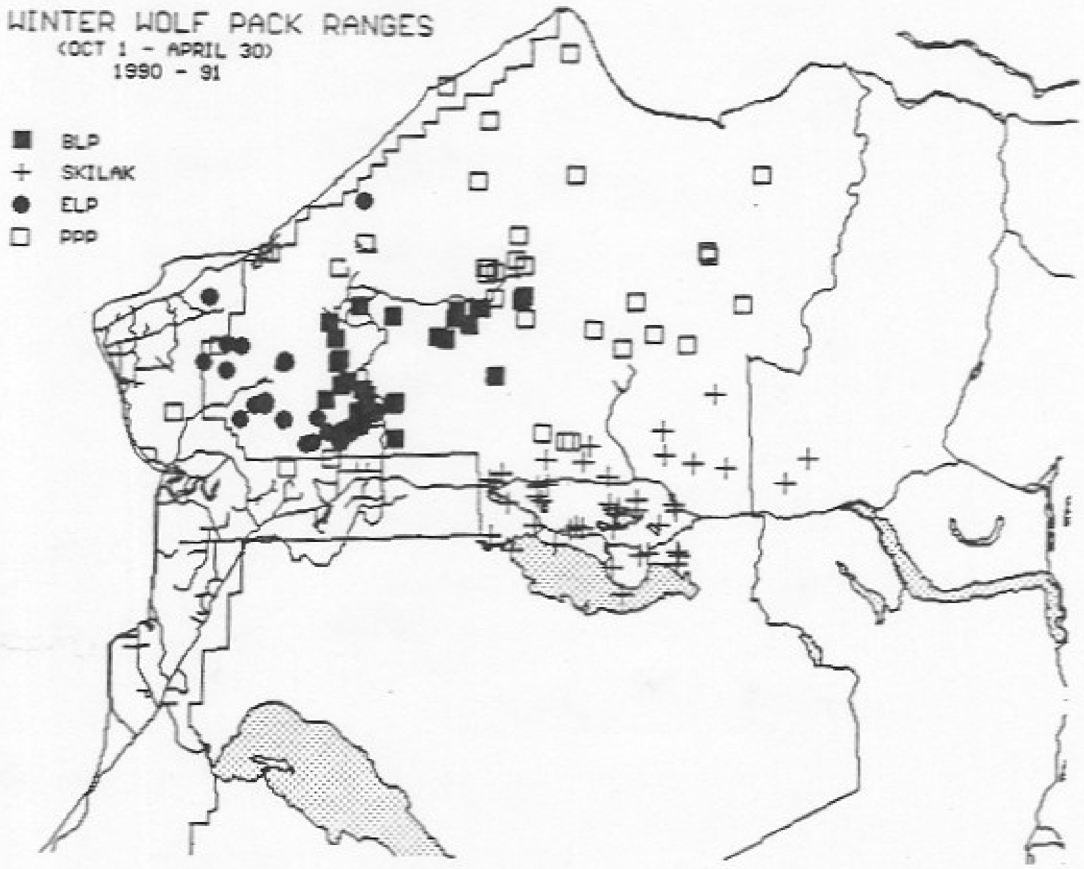
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



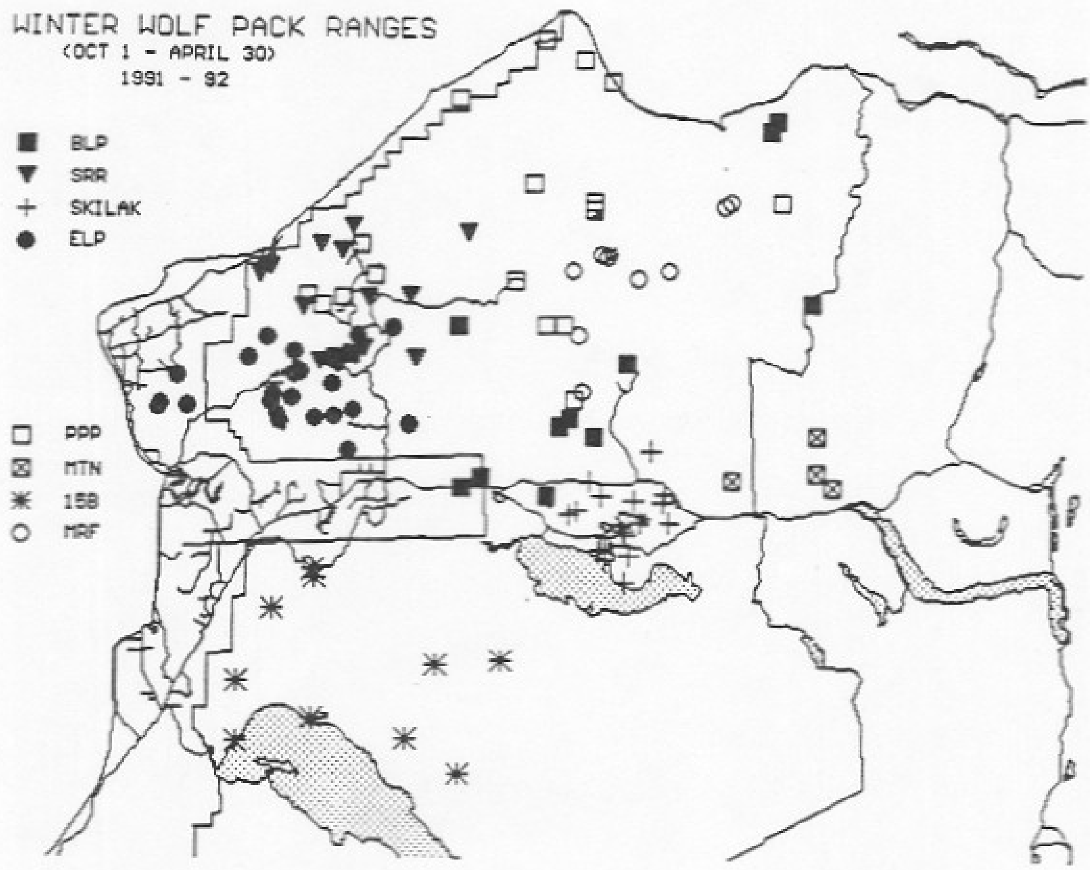
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



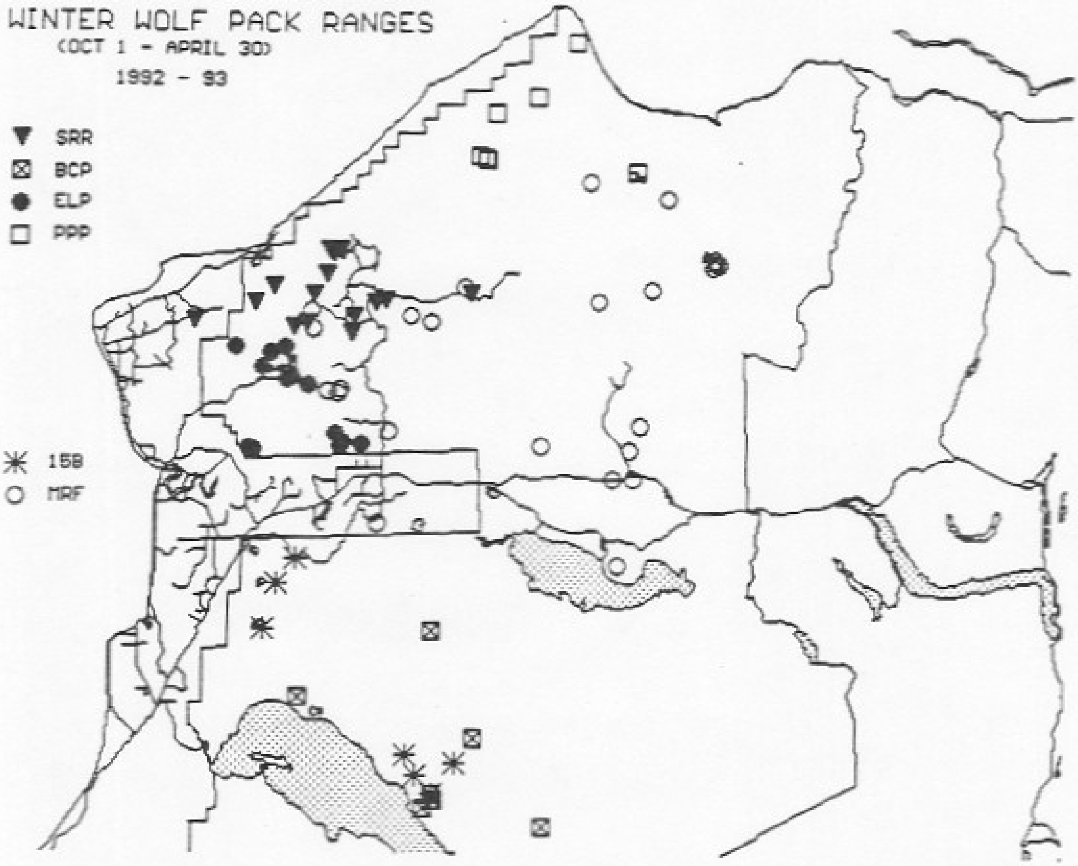
Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



Appendix 9. Yearly telemetry locations for all wolf packs monitored on the Kenai National Wildlife Refuge, Alaska, during 1982/83-1992/93.



Chapter 2

ACCURACY OF AERIAL TELEMETRY

Key words: Alaska, biotelemetry, GPS, global positioning system, habitat, Kenai Peninsula, location error, map-plotting, radio tracking.

INTRODUCTION

Radiotelemetry has been employed from the ground (Heezen and Tester 1967, Springer 1979) and aircraft (Hoskinson 1976, Gilmer 1981) for locating wildlife. Error in ground based triangulation has been reported (Hupp and Ratti 1983, Lee et al. 1985, Garrott et al. 1986, White and Garrott 1990, Nams and Boutin 1991), but the extent of error in aerial based telemetry is not well known. Sources of aerial telemetry error include the quality of maps or aerial photos, presence of landmarks, investigator's ability to locate the animal's position on a map or aerial photo, observer fatigue, search procedures, and aircraft speed and elevation (White and Garrott 1990).

Recent advances in satellite technology provide access to the Navstar GPS which is accurate to within a few cm (U.S. Department of Defense 1984, Wells et al. 1986). The position of the GPS receiver (latitude and longitude) is calculated when signals are received from $\geq$3 of 24 orbiting satellites. A 3-dimensional (3D) position (latitude, longitude, and altitude) is computed when signals from ≥4 satellites are received simultaneously, and a 2-dimensional (2D) position (latitude and longitude) is calculated from 3 satellites. Two types of signals are broadcast from each satellite, the most precise "p-code" signal is reserved for military use, whereas "C/A code" is available to civilian users, and is accurate to within 25 m (Hurn 1989). The accuracy of the civilian code is further degraded by the U.S. Department of Defense by introducing random satellite clock errors, known as selective availability (S/A), which reduce accuracy to within 100 m 95% of the time (Hurn 1989). Post-processing, or differential correction can reduce the error to 1-5 m of the true location (Stenberg and Lange 1989).

The accuracy of GPS-collected and map-plotted location data have not been compared. Several studies compared the accuracy of GPS and LORAN-C, but assumed map locations to be truth (Butler et al. 1995) or did not determine map error for their locality and assumed a +/- 20 m error (Leptich et al. 1994) between the observed location and the map location. Map error can be ≥340 m from truth (Brew et al. 1993). My objectives were to compare the accuracy of aerial GPS locations to hand-plotting aerial locations on a map, and to determine if accuracy was affected by habitat type and visibility of collars.

STUDY AREA

The study was conducted in the northwestern lowlands of the Kenai National Wildlife Refuge, Kenai Peninsula, Alaska. This area was chosen primarily because of road access to 3 habitats where radiocollared wolves

(*Canis lupus*) were located. The 1947 burn habitat consisted of dense black and white lowland spruce (*Picea mariana* and *P. glauca*) with a thick 4-5 m high canopy. The 1969 burn habitat was composed of young 3-4 m tall paper birch (*Betula papyrifera*) and aspen (*Populus tremuloides*) in a relatively open stand with little canopy cover. The mature hardwood habitat contained large stands of >40 year old paper birch, aspen, and a few black and white spruce, relatively little open ground vegetation, and thick 15-20 m tall canopy cover.

METHODS

Six trials were conducted between 13 July 1993 and 16 August 1994 to test the accuracy of aerial telemetry locations obtained using GPS and the map plotting technique. A trial consisted of 12 (164-167 MHz) wolf radiocollars (Telonics, Mesa, Arizona) with 4 collars selected randomly for placement in each of 3 habitat types. Collars were placed at locations randomly chosen from a 1:63,360 topographic quadrangle of 160 map points in each of 3 habitat types determined accessible by foot or canoe. The distance and direction to the collar location from a road or lake shore was determined with the use of an aerial photo and compass. Collars were placed in an area of approximately 1,000 km^2 and all collars were >25 m apart, and <3 km from the road. After collar locations were chosen, two of 4 collars in each habitat type were chosen randomly as "visual" collars and 2 as "non-visual" collars. A 1.5 m x 1.5 m orange tarp was centered on the ground under the "visual" collar, and could be seen from the aircraft. All collars were elevated 60 cm above ground and fitted around a plastic bottle filled with saline solution to simulate signal absorption by an animal's body (Hupp and Ratti 1983).

The "true" ground position of radiocollars in 2 trials in 1993 was estimated by averaging location data collected with a Garmin Survey II GPS receiver (Garmin, Lenexa, Kansas) with an external antenna mounted to a 4.5 m pole, but locations were not differentially corrected. The "true" ground position of each radiocollar for 4 trials in 1994 was estimated by differential correction using the same Garmin field receiver and antenna, and a Garmin Survey II GPS base unit which operated concurrently <50 km from the study area at the Killey AZ benchmark which was re-surveyed in 1988 with B order accuracy. To compare the accuracy of differentially post-processed and averaged locations, collar locations in trial 4 were estimated with both techniques. Additional locations at the Killey AZ benchmark were also estimated by averaging and differential correction by placing the GPS field receiver on top of the GPS base unit to compare the accuracy of both methods on a known point. I also calculated GPS error by placing the GPS base unit on the Killey AZ benchmark and the GPS field unit on 2 1st order accuracy benchmarks (Audrey and Kirt) and estimated their locations using differential correction.

Differentially post-processed and averaged position data were collected for 20 min if locations were logged in 3D mode, or >20 min when positions fluctuated between 2D and 3D mode. Each collection period of ≥20 min was considered 1 sampling occasion. If 3D positions could not be collected, I returned later the same or next day until 3D locations were available. Data were downloaded to an IBM computer for differential post processing using GARMIN PC100S2 software. Locations recorded with a position dilution of precision (PDOP) >4, and all 2D locations were eliminated by the software program. Differentially corrected points were averaged for each location.

A Cessna 206 fixed wing airplane with strut mounted antennas and the same pilot (R. Ernst) and observer (T. Bailey) were used in all 6 trials. Collars were located using standard search protocol (Gilmer 1981). Flight altitude ranged from 210 to 270 m, aircraft speed ranged from 130 to 157 km/hr, and wind velocity varied from 7 to 17 km/hr. After a radiocollar was located (either visually or by signal strength), the observer marked the position on a 1:63,360 topographic quadrangle, and the pilot recorded the position when the aircraft passed over the collar with a Trimble TNL 2000 in-dash GPS Navigator receiver (Trimble, Austin, Texas). Accuracy trials were flown when PDOP was relatively low, and the number of satellites was highest based upon daily ephemeris information obtained from a local surveyor. Locations of collars were not known to the observer and pilot prior to telemetry flights.

I estimated map error in the study area by locating 5 road intersections on topographic maps, determined their *x,y* coordinates with a digitizer, and then compared the digitized locations to the same positions estimated in the field with a GPS unit and differential correction. To determine how the radiotracking technique contributed to location error, the location of the 5 road intersections was estimated using the aircraft GPS receiver during 4 aerial flights.

Aircraft and ground GPS locations were transformed from latitude and longitude to UTM coordinates using ARC/INFO Software (ESRI, Redlands, California, version 7.0) and the North American Datum (NAD) 83. The aerial locations of collars plotted on quadrangle maps, and the map reference points were digitized in decimal degrees (ARC EDIT; ARC/INFO), and converted from NAD 27 to NAD 83 and into the UTM projection (PROJECT FILE; ARC/INFO) for comparison with GPS-collected locations. Error distance was calculated as the Euclidean distance of the observed aerial GPS or map hand-plotted location from the estimated true location.

Analysis of variance (PROC GLM; SAS Institute, 1993) using a mixed effects model was used to compare error of the 2 data collection methods and test the effects of collar visibility, habitat, and time on location error. A linear contrast was used to test the effect of time on accuracy of trials. Linear regression (PROC REG; SAS Institute, 1993) was used to determine the effect of latitude on map error.

RESULTS

Error of telemetry locations was not found to differ between the GPS ($\bar{x}$ = 139.1 m, SE = 9.65) and map ($\bar{x}$ = 168.4 m, SE = 21.9) plotting method (F = 2.39; 1, 36 df; P = 0.131), among habitats (F = 1.01; 2, 36 df; P = 0.373), or between visible and hidden collars (F = 2.91; 1, 36 df; P = 0.097) (Table 1, Appendix 1). Accuracy varied over time (F = 3.71; 5, 36 df; P = 0.008) with the

GPS technique improving in subsequent trials (contrast $F = 20.57$; 1, 5 df; $P = 0.0001$). The accuracy of both methods varied among trials ($F = 2.90$; 5, 36 df; $P = 0.026$) with least accuracy in trial 2. All visual collars were observed from the aircraft.

The distance between 17 road reference points estimated with GPS from the ground and air averaged 81.4 m (SE = 7.63, range = 17.3-133.0 m). When both points were plotted relative to the compass heading of the aircraft, all aerial-estimated locations were positioned before the "true" reference point; a line drawn through the aerial-estimated point and perpendicular to the line of flight averaged 67.1 m ($n = 17$, SE = 7.95, range = 16.5-123.5 m) before the "true" location. In 11 of 17 instances the aerial-estimated points averaged 16° (SE = 3.50, range = 0-31°) within the same heading as the aircraft. Based upon flights over road reference points at an aircraft speed of 130-157 km/hr (36-44 m/sec), the observer/pilot team activated the aircraft GPS receiver an average of 1.5-1.9 sec before passing directly over the road intersection.

The difference between the "true" and estimated location at the Killey AZ benchmark averaged 5.0 m ($n = 9$, SE = 1.47) with differential correction, and 7.0 m ($n = 10$, SE = 1.22) using the averaging method. GPS error averaged 0.6 m ($n = 2$) when the base and field units were tested by differential correction on 2 1st order benchmarks. The difference between 11 ground-based collar locations estimated with and without differential correction averaged 21.9 m (SE = 3.69, range = 4.2-48.9 m) during trial 4, and 8.1 m ($n = 9$, SE = 1.27, range = 1.1-12.8 m) at the Killey AZ benchmark. I combined the 2 types of ground-based collar locations in my analyses because differences between the 2 techniques were small. The difference between 6 locations digitized from the topographic map and estimated with the GPS unit on the ground averaged 70.5 m (range = 23.1-157.4 m), and increased with increasing latitude ($r = 0.81$, $F = 7.62$; 1, 4 df; $P = 0.051$).

DISCUSSION

I could not detect a difference in accuracy between aircraft GPS and hand-plotted map radiocollar locations. Locations obtained with the aircraft GPS contained error from several sources. Real-time differential GPS software for aerial surveying has been used (Bobbe 1992, Anthony and Stehn 1994) but was not available in this study, therefore aerial GPS positions included S/A error when active. The accuracy of the TNL Navigator GPS receiver is reported at <15 m (Trimble 1992) excluding error introduced by S/A. The observer/pilot team contributed error by activating the aircraft GPS receiver before they were positioned directly over the road reference points, and thus likely activated the GPS unit before flying over telemetry collars, and thus added error. My study area contained prominent landmarks such as roads and lakes which were easy to identify from the air and aided in plotting locations on a map, therefore my map-plotting error may be less than in other areas with fewer landmarks.

The observer/pilot team located hidden collars from the air as accurately as visible collars. I expected visible collars to be located more accurately from the air because the true location was observed, and not estimated with telemetry. I speculate that differences in accuracy due to collar visibility could not be determined because error in locating road reference points averaged 81.4 m, and this error probably swamped any differences.

Habitat type did not influence the accuracy of locating collars using the map-plotting or GPS method. Accuracy of aerial GPS locations was not influenced by canopy because the aircraft was above the habitat, and in direct line of sight of satellites. The estimated "true" GPS locations determined from the ground, however, may have been affected by canopy type. Rempel and Rodgers (1997), Moen et al. (1996, 1997), and Rempel et al. (1995) reported the accuracy of GPS collars decreased in denser habitat and in hardwood canopies. Deckert and Bolstad (1996) reported decreased accuracy of GPS receivers at conifer sites.

I used 1 pilot and 1 observer in 1 geographical area to compare accuracy of aerial telemetry. To determine external validity of my findings, additional pilot/observer teams should be tested at my study area and in other geographic areas. Gantz and Stoddart (1997) and I found that accuracy of pilot/observer teams increased with experience, thus experienced teams should be used for aerial telemetry. The aerial telemetry accuracy reported in this study should also be extrapolated to free-ranging animals with caution because Mills and Knowlton (1989) reported higher accuracy when observers knew that they were being tested.

MANAGEMENT IMPLICATIONS

I recommend the use of aerial GPS over the map plotting technique for locating radiocollared wildlife even though error was similar for the 2 methods. The GPS method does not require converting map locations to a usable format which is labor intensive, and data can be easily downloaded into a Geographic Information System (GIS) for analysis. Aerial GPS accuracy likely would increase if test trials are conducted to determine the optimal time to activate the aircraft GPS receiver prior to data collection and if slower, more maneuverable aircraft are used. The accuracy of GPS aircraft receivers potentially could be improved if real-time differential correction is implemented, or if S/A error is removed by the U.S. Department of Defense for civilian users.

Map error should be determined for each study area if GPS accuracy flights are conducted on reference points estimated from map locations. Map error should also be evaluated particularly if animal locations are map-plotted, and subsequently entered into a GIS system with other locations collected with GPS. I found map error to be significant for 1:63,360 topographic quadrangles which were last revised and field annotated in 1975 and 1980, respectively.

LITERATURE CITED

Anthony, R. M., and R. A. Stehn. 1994. Navigating aerial transects with a laptop computer map. Wildlife Society Bulletin 22:674-676.

Bobbe, T. 1992. Real-time differential GPS for aerial surveying and remote sensing. GPS World 3:18-22.

Brew, D. A., A. B. Ford, R. D. Koch, M. F. Diggles, J. L. Drinkwater, R. A. Loney and J. G. Smith. 1993. GPS versus template--Simple field and office experiments concerning GPS-determined positions and template-scaled map locations. Pages 199-205 *in* Geological studies in Alaska by the U.S. Geological Survey, 1993. U.S. Department of Interior, Arlington, Virginia, USA.

Butler, W. I., J. I. Hodges, and R. A. Stehn. 1995. Locating waterfowl observations on aerial surveys. Wildlife Society Bulletin 23:148-154.

Deckert, C., and P.V. Bolstad. 1996. Forest canopy, terrain, and distance effects on Global Positioning System point accuracy. Photogrammetric Engineering & Remote Sensing 62:317-321.

Gantz, G. F., and L. C. Stoddart. 1997. Accuracy of aerial telemetry locations in mountainous terrain. Proceedings from the forum on wildlife telemetry. Snowmass Village, Colorado, USA.

Garrott, R. A., G. C. White, R. M. Bartmann, and D. L. Weybright. 1986. Reflected signal bias in biotelemetry triangulation systems. Journal of Wildlife Management 50:747-752.

Gilmer, D. S., L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaiffer, and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U. S. Fish and Wildlife Service Resource Publication 140.

Heezen, K. L., and J. R. Tester. 1967. Evaluation of radiotracking by triangulation with special reference to deer movements. Journal of Wildlife Management 31:124-141.

Hoskinson, R. L. 1976. The effect of different pilots on aerial telemetry error. Journal of Wildlife Management 40:137-139.

Hupp, J. W., and J. T. Ratti. 1983. A test of radio telemetry triangulation accuracy in heterogeneous environments. Pages 31-46 *in* D. G. Pincock, editor. Proceedings from the fourth international wildlife biotelemetry conference. Applied Microelectronic Institute of Technology, University of Nova Scotia, Halifax, Nova Scotia.

Hurn, J. 1989. GPS: a guide to the next utility. Trimble Navigation, Limited. Sunnyvale, California, USA.

Lee, J. E., G. C. White, R. A. Garrott, R. M. Bartmann, and A. W. Alldredge. 1985. Assessing accuracy of a radiotelemetry system for estimating animal locations. Journal of Wildlife Management 49:659-663.

Leptich, D. J., D. G. Beck, and D. E. Beaver. 1994. Aircraft-based Loran-C and GPS accuracy for wildlife research on inland study sites. Wildlife Society Bulletin 22:561-565.

Mills, L. S., and F. F. Knowlton. 1989. Observer performance in known and blind radio-telemetry accuracy tests. Journal of Wildlife Management 53:340-342.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530-539.

_____, _____, _____, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659-668.

Nams, V. O., and S. Boutin. 1991. What is wrong with error polygons? Journal of Wildlife Management 55:172-176.

Rempel, R. S., and A. R. Rodgers. 1997. Effects of differential correction on accuracy of a GPS animal location system. Journal of Wildlife Management 61:525-530.

_____, _____, and K. F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59:543-551.

SAS Institute, Inc. 1993. SAS/STAT User's Guide, Version 6.09. SAS Institute Inc., Cary, North Carolina, USA.

Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. Journal of Wildlife Management 46:191-200.

Stenberg, J., and A. F. Lange. 1989. GPS, GRASS-GIS, and the Everglades National Park. Proceedings from the GRASS-GIS User's Group Conference.

Trimble Navigation, Ltd. 1992. TNL 2000/ A GPS Navigator Pilot Guide. Trimble Navigation, Limited, Sunnyvale, California, USA.

U.S. Department of Defense. 1984. Federal radionavigation plan. DoD-4650.4, U.S. Department of Defense and U.S. Department of Transportation, Washington D.C., USA.

Wells, D. E., N. Beck, D. Delikaraoglu, A. Kleusberg, E. J. Krakiwsky, G. Lachapelle, R. B. Langley, M. Nakiboglu, K. P. Schwartz, J. M. Tranquilla, and P. Vanicek. 1986. Guide to GPS positioning. Canadian GPS Association, Fredericton, New Brunswick.

White, C. G., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Whitehouse, S., and D. Steven. 1977. A technique for aerial radio tracking. Journal of Wildlife Management 41:771-775.

Table 1. Telemetry error (meters) estimated for an aerial Global Positioning Satellite System (GPS) and map plotting aerial locations in the northwestern lowlands, Kenai National Wildlife Refuge, Alaska during 1993-1994.

	Visual collars[a]						Hidden collars[a]					
	GPS			Map			GPS			Map		
Habitat[b]	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
47Burn[c]	87.9	15.0	13.8-190.8	104.8	17.3	23.5-227.2	156.3	20.8	77.6-284.5	224.1	64.7	53.4-663.8
69 Burn[d]	126.4	20.3	35.2-254.8	132.3	26.3	32.3-327.6	181.0	24.6	73.0-359.6	121.8	21.8	40.3-305.4
Mature hardwood[e]	157.7	25.8	42.6-347.4	191.9	34.5	49.2-423.8	125.0	27.8	21.0-319.5	235.7	101.2	10.3-1309.1

[a]36 visual and 36 hidden collars = 72 total locations.

[b]12 collars in each of 3 habitat types.

[c]dense low canopy.

[d]open low canopy.

[e]dense high canopy.

Appendix 1. Effect of trial, habitat (47 burn, 69 burn, mature hardwood), and collar visibility (visual, hidden) on location error of map hand-plotted and GPS-collected locations for 6 trials in the northwestern lowlands on the Kenai National Wildlife Refuge, Alaska during 1993-1994.

Source	MSE	df	*F*	*P*
trial	75175.6	5	3.71	0.008
habitat	20562.5	2	1.01	0.373
visibility	58990.7	1	2.91	0.097
habitat * visibility	26436.1	2	1.30	0.284
trial * habitat	23341.8	10	1.15	0.354
trial * visibility	33270.1	5	1.64	0.174
trial * habitat * visibility	20795.2	10	1.02	0.442
error MS (collar (trial * habitat * visibility))	20274.4			
collar (trial * habitat * visibility)	20274.4	36	1.56	0.093
method	31036.4	1	2.39	0.131
habitat * method	30963.1	2	2.38	0.107
visibility * method	3880.1	1	0.30	0.588
trial * method	37719.7	5	2.90	0.026

Appendix 1. Continued.

Source	MSE	df	*F*	*P*
habitat * visibility * method	17083.3	2	1.31	0.281
trial * habitat * method	15149.0	10	1.17	0.344
trial * visibility * method	3867.9	5	0.30	0.911
trial * habitat * visibility * method	12646.0	10	0.98	0.483
error MS (error)	12990.1	36		